Mem. Qd Mus. **17**(1): 73–123. [1974]

THE BENTHIC FAUNA OF SOFT BOTTOMS, SOUTHERN MORETON BAY

W. STEPHENSON*
W. T. WILLIAMS**
and
S. D. COOK*

ABSTRACT

Fifteen sites in a relatively small area south of Peel Island were sampled in quintuplicate using an 0·1m² van Veen grab. Samples were repeated at three-month intervals for two years and in the middle of the investigations there was usually heavy rainfall.

Data were analysed by the three-dimensional method described by Williams and Stephenson (1973). This method was modified: (a) to allow tests of significance of species in site-groups and this permitted scanning of all species-in-sites data to locate 'conforming' species; (b) to allow search for an alternative site-grouping to be revealed by the 'non-conforming' species—no such grouping was evident; (c) to expand the species-times data to itself become three-dimensional and thus permit separate consideration of species-in-months and species-in-years. The method was not entirely satisfactory in delineating species-groupings; it considers variances of differences (from species-centred values). As a result species-groups were derived somewhat heuristically.

The site-groups, which revealed small scale patterns, showed an extraordinarily close similarity to the differences in sediments, and other abiotic differences between sites can be neglected. There were some significant changes in sediments during the course of the work.

Changes between years were more important than those between seasons, but the evidence that this was due to flood dilution is not convincing. The inadequacy of the sampling program with respect to temporal changes was revealed.

Species-relationships to sites, to months and to years are considered in terms of 'conformity' and 'importance' instead of dominance, constancy and fidelity. In a number of cases the same species conforms and is important and there is a Petersen-type association. The species which conform to sites often conform to one or the other time dimensions and these should not be excluded from site-analyses. Species-relationships are compared with those of other relevant investigations.

The contributions of different elements to biotic complexity is briefly discussed and it is suggested that limited environmental instability may increase diversity.

INTRODUCTION

Previous work on dredged samples in Moreton Bay (Stephenson, Williams and Lance, 1970) showed indistinct spatial associations of macrobenthic species and it was suspected

*Department of Zoology, University of Queensland, St. Lucia, Qld
**C.S.I.R.O., Division of Tropical Agronomy, St. Lucia, Qld

that the 'real' patterns in certain areas were finer than those revealed. This is in part because stations were widely spaced and rarely less than $\frac{1}{2}$ mile (0·8 km) apart, and partly because of the distance traversed in a single dredging—up to 20 m. Finer patterns were now sought and the dredge was replaced by an 0·1 m^2 van Veen grab. Because dredge and grab sample different fractions of the benthos, the present investigation is a new study in an area south of Peel Island whose complexity was indicated by the previous work,

It had been hoped to sample sites on a grid pattern at 100 m apart but this proved impossible. Eventually three main areas of sampling were selected, each containing five sites spaced so that relatively small-scale area patterns might be revealed.

The previous work stressed area patterns, but seasonal changes in certain species were noted. The present work was planned on a seasonal basis with samples at three-month intervals, thus permitting evaluation of area and seasonal effects. Seasonality has a particular importance because in the classical studies of benthic communities by the 'Petersen school' beginning with Petersen (1914), seasonally occurring species have been eliminated. Petersen himself stated (1914, p. 4) '. . . It is obvious beforehand, that every single species occurring on the valuation lists is not of the same importance . . .; many animals only occur in quantity at certain times of the year, hence called seasoned animals; from the different quantities in which they occur on the lists we are, therefore, in general not able to draw any conclusion as to the composition of the community.' Seasonal variations in benthic populations have been noted by several workers, for example Raymont (1949), Kitamori (1950) and Yamamoto (1952) but we know of no satisfactory attempts to obtain a relative measure of area and seasonal effects.

The initial intention was to sample a complete year plus one season of overlap. In the event, the proposed overlapping season (March 1971) followed an abnormally wet season which could be expected to cause a marked reduction in the biota. By extending the sampling it was possible to compare a 'normal year' with one involving recovery from a natural catastrophe. Here again a literature exists dealing with various catastrophes, for example Stauffer (1937), Parker (1955), Sandisson and Hill (1959), Dean and Haskin (1964) and Tulkki (1965).

The results indicated only a slight effect of the abnormal season, and are possibly more relevant to studies of annual changes in benthos generally. The literature which exists does not give relative evaluations of areas, seasons and years. It includes Moore (1933), Poulsen (1951), Ursin (1952), Birkett (1953), Segestråle (1960) and Kühlmorgen-Hille (1965).

As expected the survey revealed a large number of species or, in Hurlbert's (1971) terms, high 'species density'. Also there were many codominant species or, in the terms of Whittaker (1965) and Sanders (1968) high 'dominance diversity'. We could have approached the problem as a diversity study, along the lines reviewed by Whittaker (1972) but preferred for reasons given later to approach it in a classificatory context. The methodology has already been outlined (Williams and Stephenson, 1973).

AREA OF INVESTIGATION

Positions and Depths of Sites

Moreton Bay as a whole (Figure 1) has been described by Stephenson, Williams and Lance (1970) and by Maxwell (1970). In subtropical latitudes, it is partly an arm of the

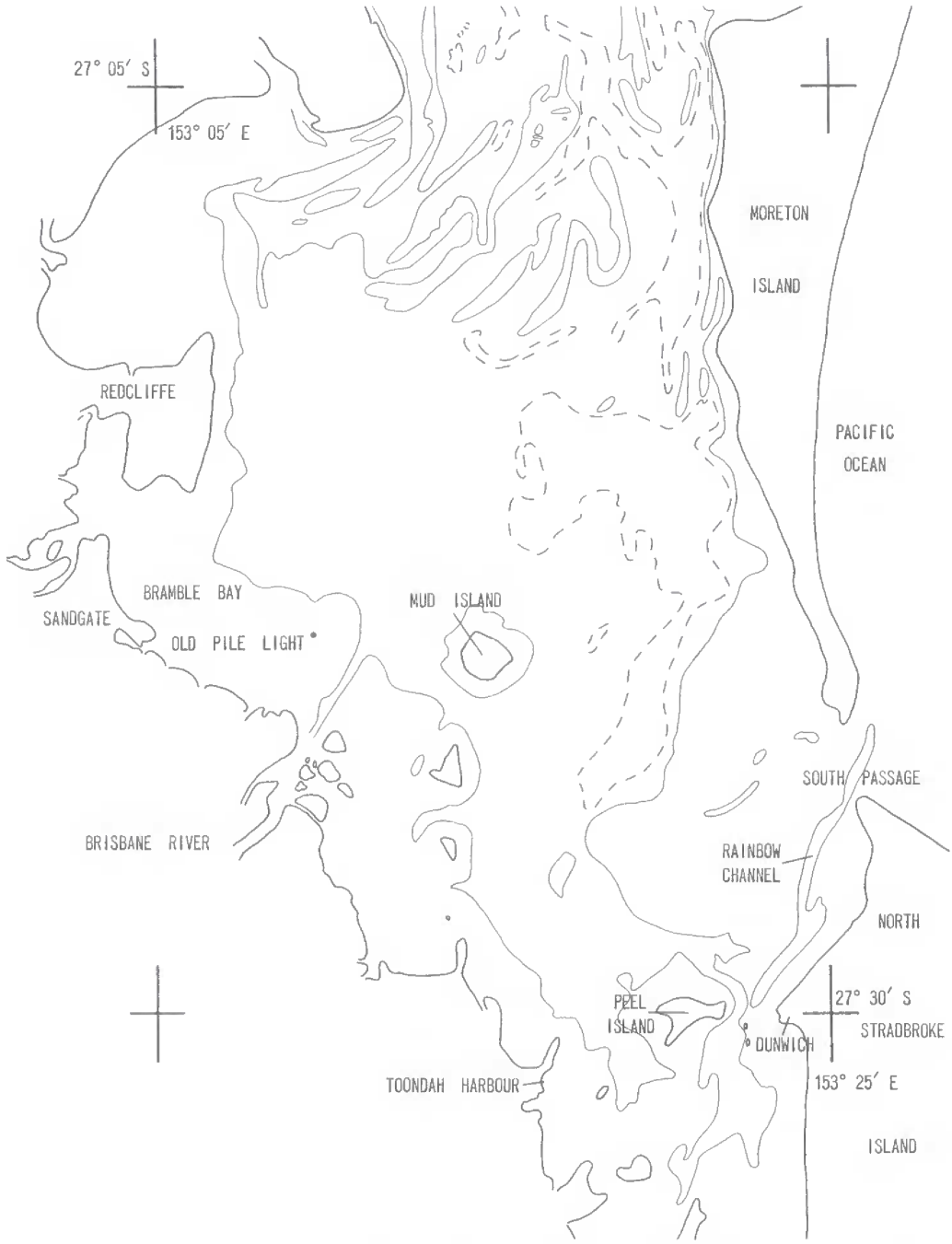

FIG. 1: Moreton Bay, showing localities mentioned in the text. Thin continuous lines = 3 fm (5·5 m); broken line = 10 fm (18·2 m).

Pacific and partly a complex estuarine system, with numerous islands in its southern portion. The present work was carried out in this southern portion and near Peel Island for the following reasons: (1) as established by our previous work, it is an area with a rich

fauna and with a small scale patterning of 'communities', (2) relative shelter minimises interruption of sampling by bad weather; and (3) there is an abundance of navigation beacons for use as sighting marks.

Choice of sites was restricted by an underwater cable and the necessity to relocate sites with speed and accuracy; this required intersecting lines of sight using nearby beacons. Finally three areas each of five sites were selected in regions with contrasting bottom topographies as revealed in the published chart of the area (Department of Harbours and Marine—Queensland—Moreton Bay, Peel Island to Russell Island, surveys to 1969). After several surveys had been completed, a checking of depths at sampling sites revealed considerable differences from the above chart. More recent data have been provided through the kindness of the above State Department ('Survey by J. K. Slater and L. V. Lee, completed 29/11/69, Dunwich to Toondah Harbour, Hydrographic Plan'). In Figure 2 sites are plotted in this plan; their positions have been established by horizontal sextant angles of conspicuous fixed points (data filed in archives of Queensland Museum).

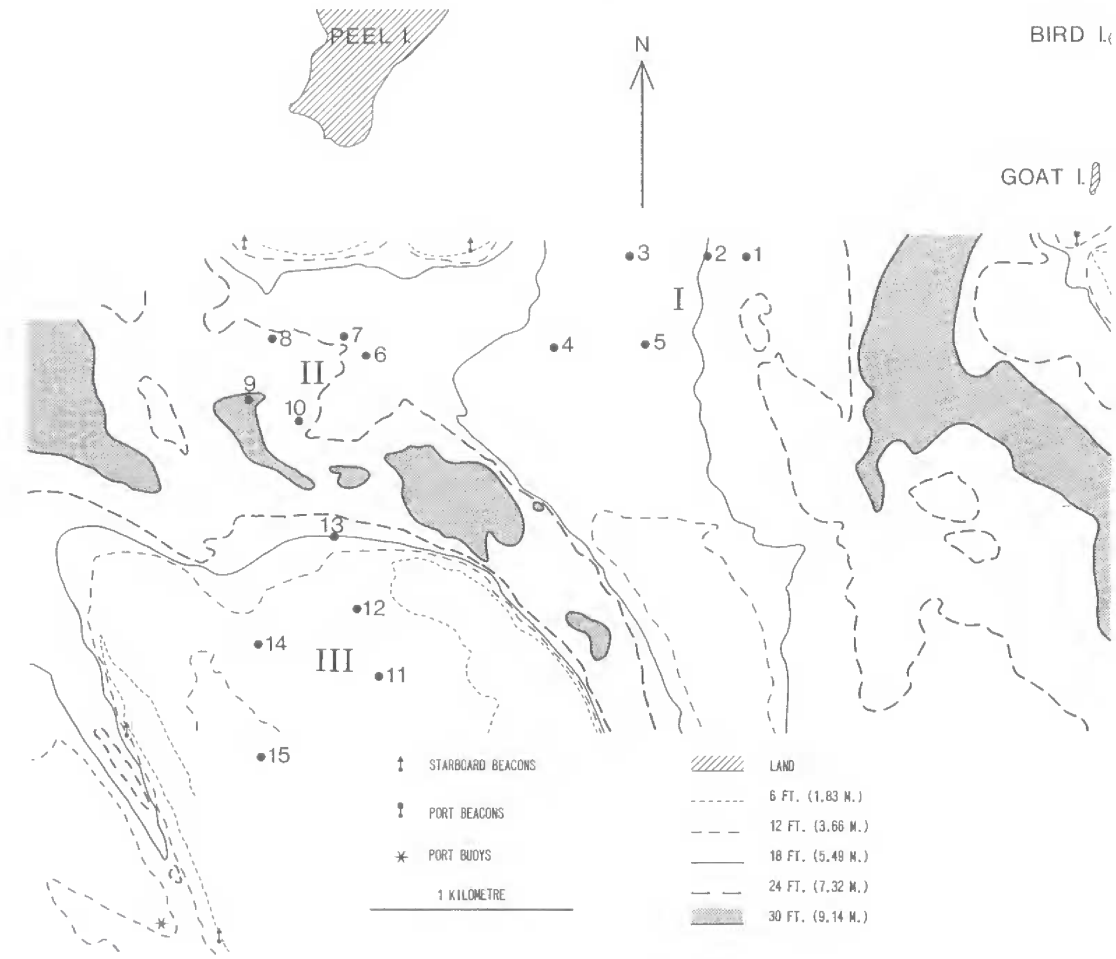

FIG. 2: Sampling sites (1–15) grouped in areas I, II and III.

Owing to the above, grouping of sites by proximity and by bathymetric features do not coincide. The proximity groupings are into a northeasterly area (I) comprising sites 1–5, a northwesterly area (II) of sites 6–10, and a southerly area (III) of sites 11–15. Areas encompass in km^2: I,0·24; II, 0·16; III, 0·36; all sites are enclosed within 3·08 km^2. Topographic grouping of sites gives: 'Goat Island slope' 1–5; 'Northwest gutter' 6–10, 13; 'Southern shallows' 11, 12, 14, 15. From the soundings on which Figure 2 is based sites can also be grouped by depths as follows: shallow (2·4–5 m) 3, 4, 5, 11, 12, 14, 15; medium (5·1–7·5 m) 1, 2, 6, 7, 13; deep (7·6–9·3 m) 8, 9, 10.

Sediments

Maxwell's (1970) results on the sediments of Moreton Bay were incorporated in the benthic studies of Stephenson, Williams and Lance (1970). In the present investigations it was found necessary to re-investigate sediments primarily because Maxwell's stations were too distantly spaced; for example they failed to reveal the muddy substrata in Area I.

About 5% of each grab sample was carefully hand sorted for specimens and used for sediment analysis. This was performed by elutriation methods with the pore sizes of sieves as follows in mm: 1·98, 1·02, 0·53,0·15, 0·211, 0·099. The grades retained are here described as gravel, very coarse sand, coarse sand, medium sand, fine sand and very fine sand respectively, and the non-retained grade as mud.

TABLE 1

Mean Percentages of Sediment Grades, from Quintuplicate Samples March 1970 and December 1971.

Sites	Gravel	V. coarse sand	Coarse sand	Med. sand	Fine sand	V. fine sand	Mud
1	1·41	0·53	0·58	0·59	2·77	37·30	54·86
2	4·25	1·47	1·22	1·08	1·02	33·08	57·96
3	4·33	1·58	1·51	1·23	1·09	30·91	59·02
4	4·03*	1·01	0·96*	1·18*	2·31	47·61	42·55
5	3·24	1·22*	1·25*	1·86*	2·20*	35·25*	56.51
6	4·87*	5·19	17·14	34·78	35·10	6·47	14·08
7	10·94	10·22*	19·56	25·01	13·80	6·25	14·16
8	10·31*	10·08	19·68	24·50	12·63	7·50*	15·16
9	13·34	7·86	14·06	21·47	20·04	9·54	15·92
10	13·51*	8·25	14·52	19·40*	15·92	9·14	15·16
11	8·84	1·49	1·52	8·20	49·91	16·35	13·06
12	6·51*	1·08*	1·33*	8·67	35·48*	20·32	26.66
13	13·34*	10·96*	11·59*	14·75*	18·13*	17·95*	13·60*
14	7·50*	3·23*	5·03*	11·02*	40·33	28·15	25·02
15	5·28	1·45	2·03	15·57*	35·89*	19·43*	17·36*

*These values showed significant differences between the March 1970 and December 1971 samplings.

The main sets of samples were collected in quintuplicate at the beginning (March 1970) and end (December 1971) of the biotic sampling. An additional set was taken in March 1971 when, following the floods of 1970/71, a soft sediment layer in 5 mm thick was noted in area I. Single analyses performed on this surface layer at each of the sites 1–5, showed little change from March 1970 apart from a slightly increased percentage of fine sand and decreased percentage of mud.

Comparisons between March 1970 and December 1971 showed significant changes in many of the fractions (those affected are asterisked in Table 1). The important changes are: Stn 5, less mud; Stn 12, less fine sand and more mud; Stns 13 and 14, more very coarse and medium sand and less mud; Stn 15 less coarse, medium and fine sand and more very fine sand and mud. There is no consistent pattern in changes excepting their concentration in area III.

Mean values from the two main sets of analyses are given in Table 1. To facilitate understanding the grades in this Table are fused, giving: coarse sand comprising medium sand and grades coarser; fine sand (including very fine sand); and mud. The sediments may then be classified by the mode (using fused grades) and further subdivided by mud percentages as in Table 2.

TABLE 2

DISTRIBUTION OF SEDIMENTS CLASSIFIED BY MODE AND MUD PERCENTAGE

Mode	% Mud	Sites
Mud	>50	1, 2, 3, 5.
Fine sand	50–25	4, 12, 14.
	<20	11, 15.
Coarse sand	<20	6, 7, 8, 9, 10, 13.

Further perusal of data indicates that the most aberrant sites in the first, third and fourth groups are 1, 4 and 13 respectively. If required the fourth groups can be further subdivided by percentages of coarse sand into 6, 7, 8, with >60% and 9, 10, 13 with <60%.

WATER MOVEMENTS

North of Peel Island tides flood from and ebb to the north. Immediately south the tidal streams come from northeast and northwest round the island, leaving a 'slacker' area which includes area I. Conversely in area II the tidal currents are strong and during spring tides surface currents are 2–3 knots. No data are available on bottom currents.

The area as a whole is protected from oceanic swells and waves are due solely to local winds. The most relevant data are the annual wind-roses for Brisbane given in the Official Year Book of the Commonwealth of Australia for 1970. At 9 a.m. the most frequent winds are southerly and southwesterlies, while at 3 p.m. they are most frequent in an arc from northeast to southeast. Newell (1971) also includes wind data from Sandgate covering January 1967 to December 1968 and states (p. 5): 'A seasonal pattern emerges, with winds from north to east predominating between December and April, and from south to south-west between May and August. There is no obvious seasonal pattern in the occurence of strong or light winds.'

The longest wind-fetches in the sampling area are in an arc from south to southeast and the wave-action is severest when these winds blow against a flooding tide from the north. This and the shallow depths makes sites 11, 12, 14 and 15 the most wave affected. Area I is the most protected, particularly from the north-northwest and north; next is area II especially from the north-northeast. From all other northern directions waves curve round Peel Island to affect all areas.

SOURCES OF WATER IN THE AREA: Newell (1971, p. 31) notes that the southern end of Moreton Bay is relatively isolated from the aspect of water exchanges and notes that '. . . the Bay water is divided into an eastern fringe, a western and southern fringe, and a central zone.'

General observations supplemented by drogue data of Helbig (unpublished) shows that a stream of eastern or Pacific water enters the area from the South Passage via the Rainbow Channel with incoming spring tides. This will give the most oceanic influences in area I. The tidal flow into areas II and III is more from the western and central portions of the Bay which are under greater terrestrial influence. Newell (1971) has shown this includes greater dilution by flood waters and a greater temperature variation—it also includes higher turbidity and greater possibilities of pollution.

Newell's (1971) work did not encompass the occasional catastrophic effects of severe flooding from river run-off, which have been mentioned by Slack-Smith (1960) in a biological connection and Stephenson (1968) in a brief hydrographical survey. The main influence of floods in the area is from the Logan-Albert River which discharges from the south. These effects will be greatest in area III, and least in area I. This topic is further discussed under seasonal changes (see below).

SEASONAL CHANGES

DILUTION AND CONCENTRATION

No direct data are available on salinities within the area of investigation, but relative effects can be deduced from rainfall data and water discharge by the Logan-Albert Rivers. Unfortunately data upon flows in these rivers does not cover a sufficiently long and continuous period to be of present value. Rainfall data, kindly supplied by the Commonwealth Bureau of Meterology have been used. From the known rainfall pattern in the Logan-Albert catchment two weather stations were selected as typical of lower and higher rainfall areas; these are Beaudesert and Springbrook respectively. (In fact Springbrook is just outside the watershed but is still regarded as typical of the higher rainfall areas). Data upon monthly rainfalls at these sites from 1915 onwards are given in Table 3. From December to March is typically the wet season, and July to September is typically the driest part of the year.

Analysis of the total available rainfall data from the above stations showed that the year before the study (1969) was fairly typical except for an increase in August recordings. The late autumn and winter of 1970 (May–August) and of 1971 (April–June) were unusually dry and from this one would expect higher than usual salinities in the sampling data. The summer of 1970–71 (Dec. 1970–Feb. 1971) included two months of exceptionally heavy rainfall from which one would expect unusual summer dilution. Comparably ususual

TABLE 3

RAINFALL IN 1/100TH INCH FOR SELECTED SITES IN CATCHMENT OF LOGAN-ALBERT RIVERS.

Month	Beaudesert				Springbrook			
	Mean* (St. Dev.)	1969	1970	1971	Mean* (St.Dev.)	1969	1970	1971
Jan	514(361)	238	796	801	1680(1376)	181	1116	1646
Feb	529(445)	99	487	1173	1809(1468)	1037	1964	3823
March	397(288)	75	470	143	2310(2978)	1197	1022	1743
April	241(212)	65	82	23	1039(817)	237	501	611
May	204(226)	838	63	88	828(681)	1643	126	147
June	245(286)	83	70	22	799(1081)	111	67	91
July	177(199)	90	64	108	603(842)	184	160	295
Aug	137(114)	527	42	155	390(339)	539	202	339
Sept	163(121)	127	274	148	408(306)	167	504	237
Oct	274(200)	543	314	109	613(475)	2188	987	243
Nov	312(233)	334	499	306	830(697)	1480	1405	416
Dec	478(298)	332	1204	244	1037(789)	398	3125	728
Total	3680	3351	4365	3320	11975	10462	11179	10234

*Means and standard deviations are for 1915–1970 inclusive.

conditions, in both respects (low and high rainfalls), have not occurred since 1946–47, and for these reasons one might expect particularly accentuated seasonal patterns in the benthos.

TEMPERATURE

The most relevant available data are mean monthly temperatures at the Pile Light off the mouth of the Brisbane River, covering the period 1931–1950.

TABLE 4

WATER TEMPERATURE IN °C AT (OLD) PILE LIGHT.

Month	Mean	Highest	Lowest
Jan.	25·6	27·8	23·9
Feb.	25·0	28·3	23·9
Mar.	25·0	26·1	23·3
Apr.	22·8	25·0	21·1
May	20·6	23·3	18·9
June	17·8	22·2	15·6
July	16·1	18·3	14·4
Aug.	16·7	18·9	14·4
Sept.	18·3	22·2	16·7
Oct.	21·1	22·8	19·4
Nov.	22·8	25·0	21·7
Dec.	25·0	26·7	22·8
Mean	21.1	22.8	20.6

These data were kindly made available by the Commonwealth Bureau of Meteorology and comprise 9 a.m. readings at depths of 6–8 ft (ca. 2–3 m) below water level. Converted to °C they are shown in Table 4.

No data are available during the years of the present study, but since there were no prolonged periods of unusual air temperatures, we may assume that the water temperature lay tolerably close to the mean values given above.

SAMPLING PROGRAM

Many authors have criticised the use of single 0·1 m² grab samples, for example Holme (1950, 1953, 1964) and M. L. Jones (1961). Clearly the number of samples required depends upon the small-scale heterogeneity of the area and Ford noted as long ago as 1923 that a slight alteration of the position of the ship sometimes gave a striking change in fauna and in substratum. Preliminary work in the present general area indicated that twenty-five 0·1 m² samples might be required at a given site. Sampling at this intensity for fifteen sites at each season was beyond the logistic possibilities, and would also have increased the risk of a second sample being collected from exactly the same area as a later one (see below). Eventually, following Steven (1930) and Longhurst (1958) five samples were taken at each site on each occasion.

Sampling was repeated at intervals of three calendar months from March 1970 to December 1971, and with one exception (March 1970) collections were made within a week. Difficulties in operating occurred initially. The boat was positioned accurately by drifting from an upwind or uptide position, but like Day, Field and Montgomery (1971 p. 7) we found the grab 'tended to strike the bottom on its side, and many attempts had to be made before the wire could be maintained sufficiently vertical for a reasonable sample to be obtained.' This was overcome firstly by working only during neap tides, secondly by not operating in wind speeds exceeding 20 knots, thirdly by using an anchored boat, and fourthly by lowering the grab gradually until within about 2–3 m from the bottom. With this method, the grab worked successfully in the present range of depths and substrates, excepting that repeat samples were sometimes required in area III (see later).

Problems of accurate relocation of sites arose as the work progressed. Although accuracy had been required it was discovered that only the boat anchor had been carefully positioned on each occasion. It was estimated that, owing to swinging in wind and tide, samples at each season were within an area of ca. 25 m², but that over the entire program they lay within a circle of just under 20 m radius, i.e. an area of ca. 1000 m². (On Figure 2 these circular areas are drawn to scale). Clearly some of the differences apparently due to seasons could be from sampling a different portion of the circular area.

The inaccuracy of site relocation has a counter-balancing fortunate effect. It greatly reduces the chance of the grab collecting a presampled spot. On only one occasion was there evidence (from the physical appearance and faunistic contents of the sample) that this had happened in one of the quintuplicate samples. This was discarded and recollected. No evidence was obtained of exact resampling of a spot after a seasonal interval, and because of the large area involved this would be unlikely.

The normal method of collecting the biota from grab samples was by on-board wet sieving, with the final apertures ca. 1·2 mm square. Particular care was taken over samples

containing small specimens of bivalves and gastropods which fortunately were infrequent. The procedure was modified on grounds suspected to contain *Branchiostoma* because smaller specimens burrowed through the sieve holes, and in such cases the sample was hand sorted before the finer sieving. After collection all specimens were initially preserved in 10% formalin and within a month tranferred to the most appropriate final preservative.

In summary the sampling program allows investigation of three types of spatial patterns (a) at a given site (and a given time) within the groups of quintuplicate samples whose exact spacings are unknown; (b) between the five sites within each area, which range from 150 to 700 m apart—an alternative is between topographic groupings as listed earlier; (c) between the three areas, whose incentres are from 1400 to 2430 m apart. It also allows a variety of temporal patterns to be investigated. These include seasonal (March, cf. June, cf. September, cf. December), annual 1970 cf. 1971), and possible differences immediately after a flood (March 1971 cf. remainder).

BIOTIC DATA

Identifications

Chace (1969) comments on '. . . a major and virtually insuperable problem which plagues any ecological survey in tropical waters today; that is, the imperfect knowledge of the existing fauna . . .'. This applies to Moreton Bay, despite systematic publications referred to in our dredging work (Stephenson, Williams and Lance, 1970). Because of anticipated difficulties in identification and in recognition of species, hydroids and amphipods were excluded from the investigation; the former were also excluded on other grounds. Amphipods were present in smaller numbers than in comparable surveys elsewhere, but nevertheless their omission is unfortunate.

The problems of identification were also responsible for the selection of a relatively coarse sieve (1·2 mm square) during collecting. This excludes the smaller species where the major taxonomic problems would lie. If these small species had been included a much more complex situation than that recorded would have been obtained.

Shortage of space precluded retention of all specimens collected, so reference collections were established with at least duplication of 'species' occurring twice or more. Initially species were segregated and given 'working names' with assistance from a reference collection of most species from the previous dredging work (Stephenson, Williams and Lance, 1970) housed in the Queensland Museum. This resulted in some over-splitting, and was resolved when group experts had identified collections. Over-splitting probably remains in the Nemertea. In one case (*Euclymene*) two or possibly three species are lumped because of uncertainty regarding early discarded specimens.

Reference specimens, and when possible entire collections, were referred to group experts for identification. Without this assistance (as acknowledged later) the present study would have been very incomplete or even impossible. There remained a sizeable collection with only 'working names' or incomplete identifications, some of which are likely to be in error. These have been deposited in the Queensland Museum and the attention of taxonomic experts is invited.

Groups Excluded

In addition to those excluded because of taxonomic difficulty peneid prawns were eliminated; they are known to be common at certain seasons in Moreton Bay but a grab is an inefficient device for their collection. The few specimens which were obtained were discarded.

Acorn barnacles and limpets were recovered from superficial dead shells. These belong to the hard-bottom fauna and their distribution reflects the almost random recovery of large solid objects. All the hard-bottom fauna was excluded—serpulids, polyzoa, hydroids, most polyzoans and some algae. When species occurred on large dead shell fragments and also the substratum generally (e.g. some tunicates) they were recorded.

Form of the Data: Usually the number of individuals of each species from each grab sample was recorded, but problems arose over colonial forms. Where the numbers of discrete colonies was known this was noted, but where this was not known—for example with *Halophila* where separate shoots arise from one or several stolons—we have only obtained data in a presence/absence form. Presence was noted as for a single individual.

Material which was obviously dead was not retained. All colonies of the serpulid *Filograna implexa* (Berkeley) were excluded for this reason, as would have been most polyzoan and hydrozoan colonies but for their prior exclusion. In general, empty tubes of polychaetes were not recorded either because it was clear they had not been inhabited recently or because of uncertainty over the species. The exception was *Chaetopterus variopedatus* and when it appeared that tubes were currently inhabited, but the specimens had eluded capture, data were recorded. Complete tubes were never recovered (nor were intact specimens), and here two separate tube-ends were recorded as one worm and so was a single separate end.

Species Obtained

The 420 species are listed in Appendix I. The richness of this biota is difficult to compare precisely with that of most other surveys because of methodological differences. However, a certain number of local comparisons are possible. In our dredging work in Moreton Bay, we covered a much greater variety of habitats and a much greater area (ca. 775 km^2 against ca. 3 km^2) but obtained fewer species, 335 in all, and 25 of these are in groups excluded from the present survey. The difference mostly reflects the loss of specimens during dredging operations. Current work by Raphael and Stephenson in Bramble Bay near the mouth of the Brisbane River, using the present grab and sieves, and over an area of ca. 30 km^2 seems likely to produce ca. 180 species, thus indicating a relatively impoverished fauna. Hailstone (1972) in the lower reaches of the Brisbane River has noted 136 species from carefully sifted dredgings obtained from an area of ca. 1 km^2 (but of varied habitats).

Comparisons from wider areas are more difficult but we can note 74 species from an area of ca. 4 km^2 in a single season at Sek Harbour, New Guinea, using the present technique (Stephenson and Williams, 1971) and 264 species from ca. 30,000 km^2 by Petersen (1914) in Danish waters (Stephenson, Williams and Cook, 1972). Summarising the above, we are clearly dealing with a species richness of a different order from the other authors quoted.

At the level of actual species present, the present is a pioneer study in eastern Australian waters. Hence there are numerous new Queensland records and a considerable number of undescribed species. This renders comparisons difficult and premature, and the only relevant ones are with surveys in Moreton Bay. Comparison with the dredge survey of Moreton Bay as a whole (Stephenson, Williams and Lance, 1970) is difficult because of the unidentified species in the two surveys (e.g. sponges) and because some species were confused in the earlier study. For example we suspect at least five species of ophiuroids were recorded previously as *Amphioplus* sp. (This was due to damage of specimens during collection and examination of insufficient samples.) Within comparable taxonomic groups 115 species were common to the two surveys, 150 were obtained by dredge only and 275 by grab only. This confirms the relative inefficiency of dredge sampling and that the two methods sample different fractions of the biota.

Comparison with incomplete data of Raphael and Stephenson indicates 70 species common to the two areas, 110 only at Bramble Bay and 350 only at Peel Island. Comparisons are not affected with Hailstone's data from the lower Brisbane River, much of which is incompletely identified.

ANALYTICAL METHODS

Fusion of Samples

Analyses of small scale topographic patterning within quintuplicate samples was attempted, but because precise positions are unknown and only five samples are available at each site, analyses were restricted, and results are not detailed. There were indications of small scale aggregations in at least half of the more ubiquitous species. To reduce data to moderate proportions, results from quintuplicate samples are fused and in general represent numbers obtained from 0·5 m^2 samples. The presence/absence data upon such forms as *Halophila* now become meristic summations and hence all data are of substantially the same form.

Choice of Method

The main problem is to produce conceptual order within the 420 species obtained in the survey. It could be approached by what have become almost traditional methods of studying diversity, using one of the multiplicity of diversity measures based upon the proportions of species present for example Simpson (1949), Margalef (1951), McIntosh (1967), Edden (1971), Hurlbert (1971); or the widely used measures depending upon information theory, the Shannon and Brillouin measures (see MacArthur, 1955; MacArthur and MacArthur, 1961; Lloyd and Ghelardi, 1964; MacArthur and Wilson, 1967; Lloyd, Zar and Kar, 1968; Pielou, 1969; Whittaker, 1972). There is a comparably extensive literature upon measures of equitabllity or evenness, as quoted in Hurlbert (1971) and Whittaker (1972), and upon explanations of why diversity and equitability are higher in some situations than in others (see Pianka, 1966; Recher, 1972; and Whittaker, 1972).

We believe that the best approach is by partitioning so that, for example, we can evaluate the contributions made by species in sites, seasons and years. There have been theoretical discussions of the partition of diversity information statistics for example by

Kullback, Kupperman and Ku (1962) and by Kullback (1968) and an ecological approach by Orloci (1968). Partitioning of information diversity has been explored in an ecological (rain-forest) problem by Williams et al (1973). There are two disadvantages as listed by Williams and Stephenson (1973); partitioning is incomplete and results seem ecologically unsatisfactory. An alternative method is to use a sum-of-squares partitioning as detailed in the last quoted paper and this we followed. Because it involves analysis of variance and euclidean distances (centred), results are likely to be unduly influenced by the more abundant species. In the earlier paper a cube-root transformation was used and incomplete investigations of effects of transformations suggested this was appropriate in the present case.

Our original data is in four-dimensional form viz 15 sites $\times$ 4 seasons $\times$ 2 years $\times$ 420 species, and desirably we should seek patterns between all possible pairs of these dimensions. When analysis commenced, no method of handling four-dimensional data had been developed, so our data was first regarded as three-dimensional and in the form of 15 sites $\times$ 8 times $\times$ 420 species. (The times 1–8 run sequentially from March 1970 at three month intervals to December 1971). The three-dimensional technique is as described by Williams and Stephenson (1973) and leads to three two-way coincidence tables, of sites and species, times and species, and sites and times. Flexible sorting with β at $-0{\cdot}25$ was used (see Lance and Williams, 1967; Stephenson, Williams and Cook, 1972).

Critique of Method

We should first comment on the advantages of this method over the two approaches used previously. The first used a $qt \times s$ matrix (where q = quadrats, t = times and s = species). Analysis by any of the usual techniques of grouping samples usually reveals via the dendrograms whether the major influence is due to q or to t. Interpretation of subordinate groupings is difficult because they are variably homogeneous with respect to q and t attributes. Comparable difficulties arise if we make t separate analysis of q and s.
As quoted in an earlier paper (Stephenson, Williams and Cook, 1972) referring to work by Hailstone (1972) we stated: 'For each month of the year the data reveal site groups and species groups related through coincidence tables. But from month to month the site groups alter their composition and so do the species groups.'

Various sub-sets extracted from the present data had been separately analysed before the present main analysis began. These were the 55 species as related in Williams and Stephenson (1973), the ophiuroids (19 species) and tunicates (27 species). Details need not now concern us, the main conclusions were that the site-groupings obtained in each case were substantially similar, but the times-groupings were not. For example, with the tunicates the main picture was seasonal with grouping of times: 1 + 5, 2 + 6, and 3 + 7, but breaking down with 4 and 8. The 55 species and ophiuroids gave segregation of March data 1 + 5, with an annual pattern for the remainder, viz. 8 + 7 + 6, 4 + 3 + 2. With the 71 species selected as below yet another pattern emerged: 7, 8 + 6 + 5 + 1, 4 + 3 + 2.

It is evident that times-groupings give no overall conceptual picture. As in the case of $qt \times s$ matrices, groupings contained variable proportions of homogeneity with respect to two different variables. In the present case these are seasons (here m for months) and years (y). To resolve this difficulty one can again partition part of the data, converting

times × species into the dimensional form of months × years × species (summed over all sites) i.e. $m \times y \times s$ where $m = 4$ and $y = 2$.

In the analyses which follow we commenced with a $q \times t \times s$ matrix, and following the methodology of the previous paper affect data reduction, consider the relative importance of the different comparisons and analyse them in a preliminary way. This leads to two extensions, firstly of the species/sites relationships ($s \times q$), and secondly to the species/times ones ($s \times t$) which are expanded to three dimensions ($s \times m \times y$).

ANALYSES OF SITES × TIMES × SPECIES

First Stages of Analysis

These involve species reduction and considerations related thereto.

We begin by summating and obtaining means (cube root data) of: (a) all species over all times at each site, and (b) all species over all sites at each time. Values are given in Table 5.

TABLE 5

Mean Values, Species Summated (Cube Root Data) in Sites 1–15, and in Times 1–8.

Site	Mean n	Times	Mean n
1	0·490	1	0·814
2	0·473	2	1·583
3	0·456	3	1·593
4	0·671	4	1·394
5	0·457	5	0·832
6	0·883	6	1·188
7	0·785	7	1·769
8	0·775	8	1·140
9	0·749		
10	0·739		
11	0·672		
12	0·664		
13	0·840		
14	0·806		
15	0·852		

The values in Table 5 are measures of total populations and are the transformed numerical equivalents of total biomass. These data already show some 'ecological sense', for example that (a) populations are least in the muddy sites 1, 2, 3, 5 and (b), a clear seasonal pattern exists with low populations in March, rising through June to a maximum in September and declining in December. Comparison of March 1971 (time 5) with March 1970 (time 1) fails to show the expected effects of the summer flood but there is possibly a delayed effect at June 1971 (time 6 cf. time 2).

The second step leading to species reduction is to determine the contribution each species makes in terms of squared euclidean distance to the differences between all pairs of sites—i.e. to site classification. Based upon these contributions we can have a method of species reduction which is quantified and can be subject to a single decision. In the

earlier work, using 55 species, we showed an objective sum-of-squares chopping was much too drastic, replaced it by an arbitrary level and excluded species contributing less than 1% of the total variance. With the present full number of species (420) this would have left only 26 species. We reduced the level to 0·5% and retained 48 species.

In a similar way the contributions of each species to a time classification were evaluated, and taking the 0·5% level we retained 52 species. In the analysis detailed below we considered the 71 species which were present in one or another of the above lists. They are listed in Table 6 with only the generic name given when a single species of a genus is in the main list (see Appendix).

TABLE 6

71 Species List, the New Arbitrary Number is Given Followed by the Original Number in Parenthesis.

1	(1)	*Discobotellina*
2	(29)	Nemertea—"pink"
3	(35)	? *Euleanira*
4	(36)	*Leanira*
5	(37)	*Sthenelais*
6	(58)	*Arabella*
7	(62)	*Eunice antennata*
8	(63)	*E. cf. indica*
9	(70)	*Onuphis* sp. ("long gill")
10	(73)	*Chloeia*
11	(74)	*Eurythoe*
12	(75)	*Glycera americana*
13	(76)	*G. prashadi*
14	(77)	*Goniada*
15	(90)	*Nephtys*
16	(91)	*Amaeana*
17	(95)	*Loimia medusa*
18	(100)	*Pista* sp.3
19	(104)	*Terebellides*
20	(123)	*Chaetopterus*
21	(129)	*Euclymene*
22	(134)	*Magelona* sp.
23	(139)	*Petaloproctus*
24	(145)	*Spiophanes*
25	(159)	*Alpheus distinguentus*
26	(164)	*Axius*
27	(165)	*Callianassa*
28	(204)	*Carinapseudes*
29	(214)	*Columbella*
30	(221)	*Herpetopoma*
31	(236)	muricid 2
32	(244)	*Dentalium*
33	(258)	*Cycladicama*
34	(262)	*Modiolus ostentus*
35	(263)	*Ensiculus*
36	(265)	*Fulvia*
37	(267)	*Gari venta*
38	(269)	*Laternula*
39	(270)	*Leptomya pura*
40	(279)	*Malleus*
41	(283)	*Neosolen*
42	(285)	*Nucula astricta*
43	(288)	*Paphia gallus*
44	(289)	*P. subrugata*
45	(297)	*Placamen tiara*
46	(306)	*Tellina lilium*
47	(308)	*T. cf. solenella*
48	(316)	*Tucetilla*
49	(328)	*Golfingia*
50	(330)	*Thermiste*
51	(340)	*Amphioplus depressus*
52	(341)	*Amphipholis loripes*
53	(342)	*Amphioplus* sp.
54	(343)	*Amphiura bidentata*
55	(344)	*A. cataphes*
56	(350)	*Ophiocantha*
57	(356)	*Ophionereis*
58	(360)	*Hypselaster*
59	(364)	*Protankyra*
60	(367)	*Agnesia*
61	(373)	*Eugyra*
62	(381)	*Molgula exigua*
63	(382)	*M. rima*
64	(383)	*M. sabulosa*
65	(385)	*Polycarpa fungiformis*
66	(387)	*P. tinctor*
67	(390)	*Styela ramificata*
68	(394)	*Branchiostoma*
69	(413)	*Pseudocodium*
70	(419)	*Halophila ovalis*
71	(420)	*H. spinulosa*

The noteworthy groups are polychaetes (22 spp.), bivalves (16), tunicates (8) and ophiuroids (7); the noteworthy exclusions are all of the sponges, coelenterates and crabs, and all but one of the algae.

Relative Importance of Each Comparison

Using the 71 species, mean variances per comparison, as shown in Table 7, permit assessment of the relative importances of each comparison.

TABLE 7

Mean Variances per Comparison

Nature of Comparison	Variance attributable to: sites	species	times	interaction
inter-sites	—	1·629	0·905	0·406
inter-species	1·629	—	1·123	0·406
inter-times	0·905	1·123	—	0·406

These data show that, with respect to species, site-groupings are about 50% more important than times-groupings. The site-times combination, which concerns the 'numbers' equivalent of the total biomass, is about 80% of the species-times combination. Its magnitude indicates that there are important chronological changes in total populations, as discussed earlier. The interaction is the variance left in the system when any two of the major variables have been eliminated. It is the smallest value in the table and is not readily amenable to commonsense ecological interpretation so is neglected.

Site-Species Relationships

Classifying the sites by the 71 species (fused over all times) and taking this to the four group level gives: I = 11 +15, II = 6 + 7 + 8 + 9 + 10 + 13, III = 4 + 12 + 14, IV = 1 + 2 + 3 + 5. These are identical with those obtained in the preliminary analyses.

It is evident that there is small scale patterning within the area of study. With area I of 0·24 km^2 there is one site-group and part of a second; within area III of 0·36 km^2 there are elements of three site-groups; only area II of 0·16 km^2 appears biotically homogeneous. Further discussion of the site-groups is given later.

To determine how these site-groups are characterised by species, reference was made to the 2-way table, referred to in Williams and Stephenson (1973) as the *B* table which gives single values—these are the means of site-centred and species-centred deviations. Perusal suggested that many species-groups derived in the analyses were heterogeneous, and we reverted to the tables with double values i.e. site-centred values used in site classification and species-centred values for the species classification. Using the latter the species-groups now appeared more homogeneous internally, but still insufficiently so in some cases. While many species-groups contained species which conformed 'crisply' to the site-groups in others the sorting was more 'blurred'. A measure was sought of the extent to which species conformed to the site classification.

In general, the attributes used to define a numerical classification cannot be used as the basis for between-group tests of significance, since their differences have been optimized. It follows that the site-centred values could not be used for this purpose; it remains to consider whether the species-centred values can be used in their place. Unfortunately, the setting up of a two-way table implicitly assumes that the two sets of values are related, so that the between/within variance ratios will be conservative, not random, estimates. However, the variance ratio F can still be used as a measure of the extent to which a given species defines the different site-groups, and the values associated with the usual probability estimates can be taken as convenient points on an arbitrary scale. We shall henceforth refer to such tests as 'significance tests' for the sake of brevity; but it must be remembered that, though they are less biassed than would be the corresponding ratios obtained from the site-centred values, they are still biassed.

Using the above test for four site-groups and 15 sites, F values are as follows: 0·05–3·59, 0·01–6·22, 0·001–11·56. Although these values are conservative they can be used to grade species with respect to site-group conformation. Four grades were recognised with F values as follows: VH $>$ 11·56, H 11·56–6·22, M 6·21–3·59, and L $<$ 3·59.

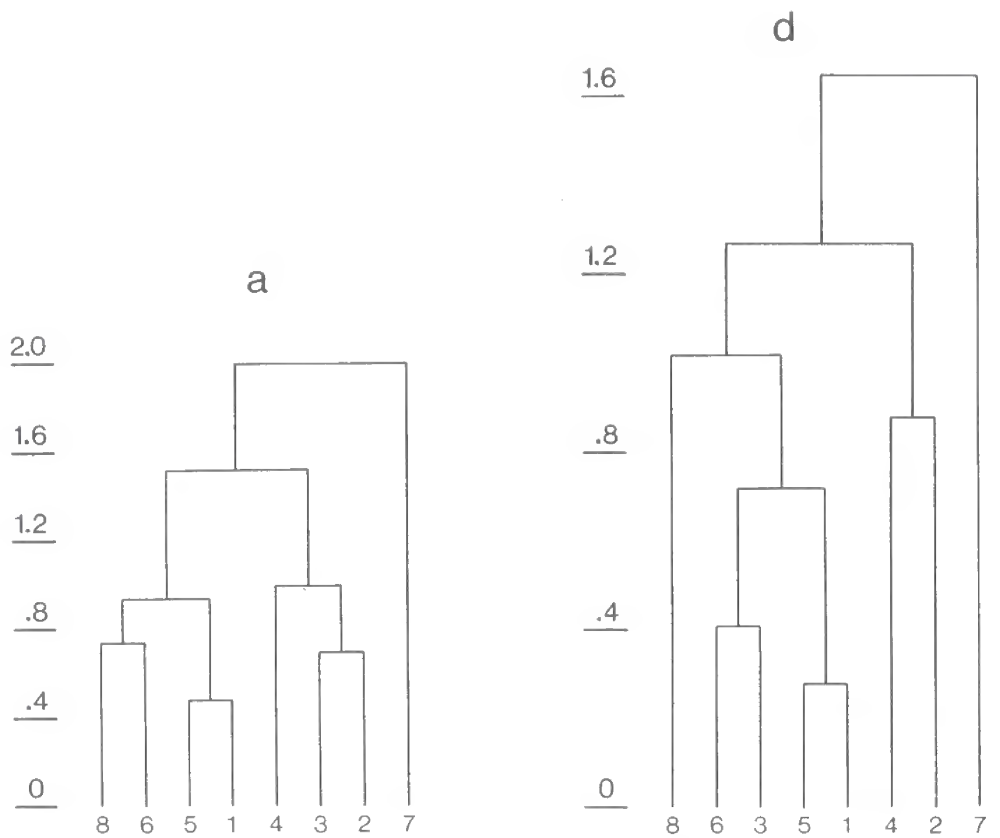

FIG. 3: Dendrograms showing classification of times by species (a) and sites (d); euclidean distance type of coefficient.

Of the 71 species classified, 22 were in the L grade, and this included species high on the list of contributions to site variance. Consideration of these and other species is given later.

Times-Species and Times-Sites Relationships

Using the 71 species list, four classifications were derived: (a) times by species, (b) species by times, (c) sites by times, and (d) times by sites. We consider first (a) and (d) above as shown in Figure 3.

In both cases the nearest pair of seasons (months) are 1 and 5 i.e. the 'normal' March of 1970 and the 'abnormal' March of 1971 immediately after the flood. It is evident that the immediate effects of the flood were minimal both on the total populations present (dendrogram d) and on the actual species present (dendrogram a).

In both cases the most isolated time is 7 (September 1971), suggesting a delayed flood effect. However in the times by sites analysis this time is characterised by a specially *abundant* total population. If there is a delayed flood effect it seems to have operated by allowing a transient increase in certain species which becomes evident after a delay of about nine months.

In neither case does the first or second dichotomy reflect a clear seasonal grouping or a clear annual grouping to indicate which factor is the more important. For this and other reasons stated earlier the analyses were expanded.

EXTENSIONS OF ANALYSES OF SPECIES-SITES

Possibility of Alternative Site-Grouping

Of the 71 species previously analysed it was considered that the 22 not fitting into the site-grouping earlier obtained, might conform to a different grouping. These species plus additional ones relatively high in the site variance hierarchy (= 34 in all) were used in a site reclassification. The site-groupings obtained were: 1 (very isolated), 12 + 14, 2 + 3 + 4 + 5, 13 + 15, 6 + 7 + 8 + 9 + 10 + 11. These do not reflect any obvious abiotic attributes nor an overall topographic pattern. Five of the six species highest in the variance hierarchy dominated the classification and gave almost individualistic distributions within the site-groups. While it is possible that another and more meaningful pattern would emerge if they were removed and the remainder re-analysed, it was considered more likely that yet more individualistic patterns would emerge. It was concluded that there is only a single important pattern of site-groupings.

No further mention is made of the species which failed to fit the general site-groupings, unless they appear in the later times-groupings. One species which seemed to characterise the area as a whole, and which was one of the characterizing species of the earlier dredge study, is eliminated from the present groups. It is *Leanira* (36).

Consideration of Additional Species

The technique of testing species for significance of conformity to the major site-pattern was applied to all 420 species. Ninety-seven species conformed at the M grade or

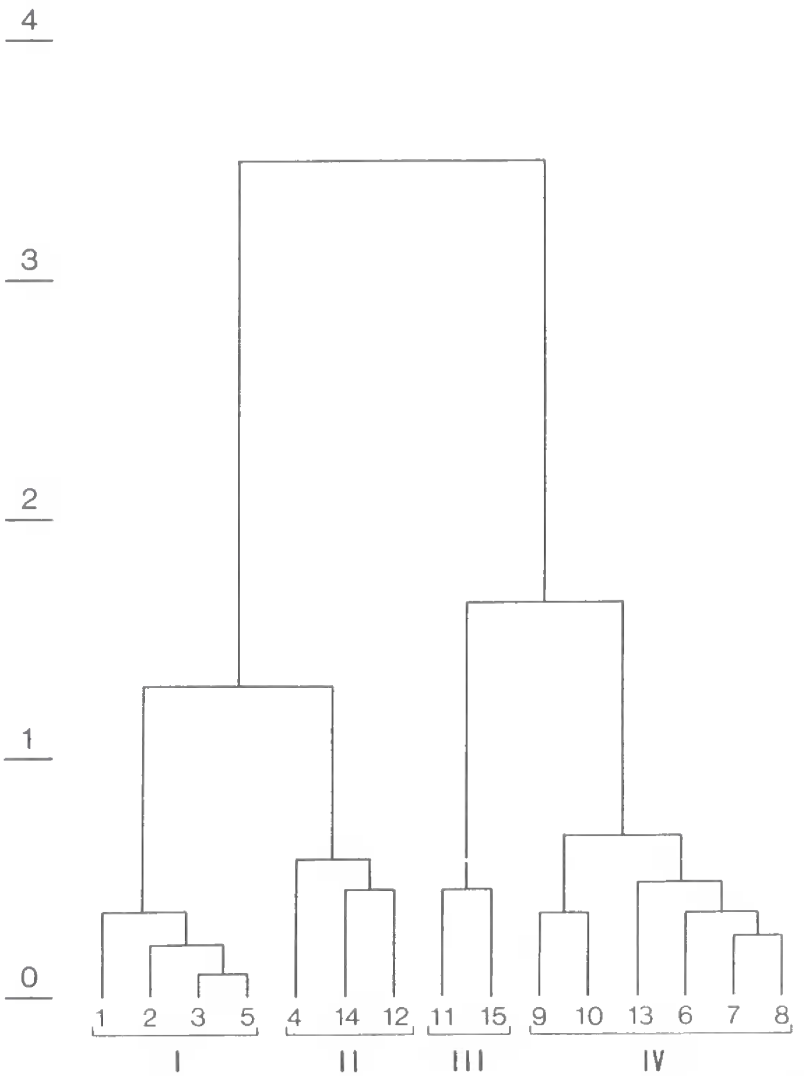

FIG. 4: Dendrogram of sites classified by 97 spp., euclidean distance type of coefficient. The site-groups (I–IV) do not refer to the area groups in Figure 2.

higher and these extended as low as 250th in the site-variance hierarchy. The matrix of 15 sites × 97 species was reclassified.

SITE-GROUPS

As expected, the four original site-groups were generated (see Figure 4) and as stated earlier these agree with those obtained using sedimentary attributes. The correspondence goes below the four group level; thus in site-groups I and II the 'aberrant' sites by both systems are 1 and 4 respectively. Site-group IV can readily be subdivided by both systems which agree in having sites 6, 7 and 8 in one subgroup and 9 and 10 in the other. The only discrepancy concerns site 13 which links with 6, 7 and 8 in the dendrogram and with 9, 10 by sediments.

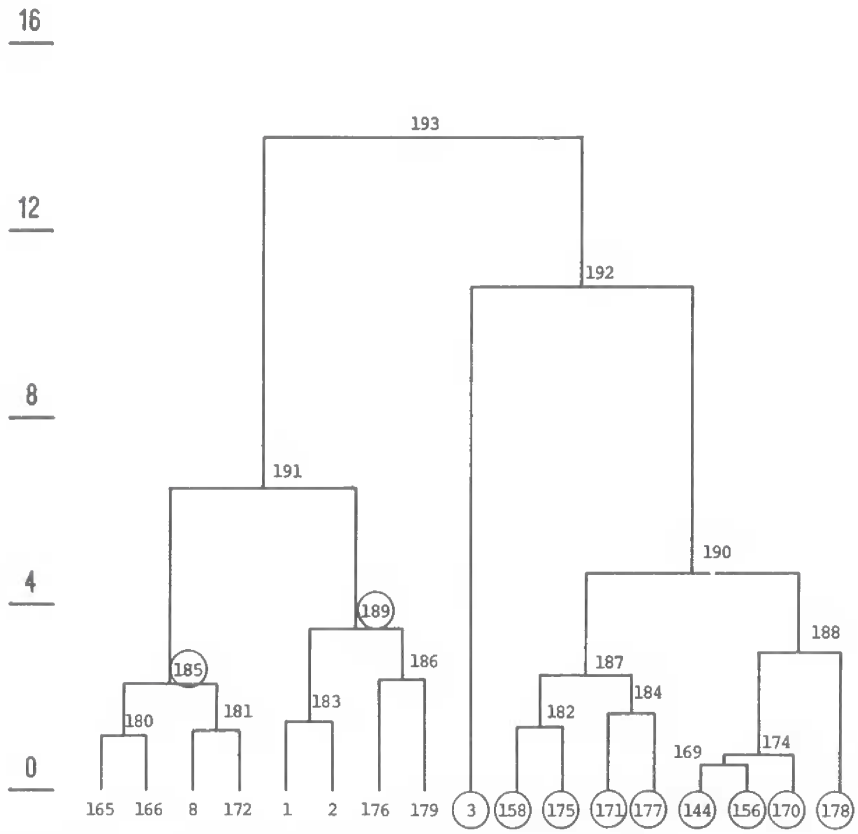

FIG. 5: Dendrogram of species-groups (involving 97 spp.) classified by sites, euclidean distance type of coefficient. The 17 groups originally considered were reduced to the eleven which are ringed.

SPECIES-GROUPS AND TWO-WAY TABLES

After generating an excess of species-groups, 17 were considered as shown in Figure 5. Further fusions within the exact framework of the dendrogram destroyed the conceptual sense of the species groupings as revealed in two-way tables. This sense was retained by accepting groups at different dendrogram levels, as shown in Figure 5, with a condensed two-way table in Table 8. In other cases we have investigated, acceptance at different levels has been due to group-size dependence, a phenomenon inherent in sharply clustering strategies such as the flexible strategy here employed. (See Williams et al, 1971 for discussion of group-size dependence). In the present case higher fusions were possible when the groups contained the more abundant species and this is discussed later.

Nine rows of Table 8 contain a single value distinctly higher than the remaining three, and here the species-groups characterize the site-groups in a positive way. Two rows contain two high values, and the relevant species-groups (189, 177) each positively characterize a pair of site-groups. There are only two possible species-groups with a single distinctly low value (189, 3) and in the discussion below we concentrate upon positive characterizations.

TABLE 8

MEAN DEVIATIONS OF SPECIES-GROUPS (SPECIES STANDARDIZED VALUES) IN SITE-GROUPS. SPECIES-GROUPS ARE AS IN FIGURE 5.

Species groups	Site-groups and sites therein			
	I 1, 2, 3, 5	II 4, 12, 14	III 11, 15	IV 6, 7, 8, 9, 10, 13
185	−1·8	−0·9	−1·6	2·0
189	−4·8	−2·3	3·5	3·2
3	−2·0	9·3	−4·4	−1·8
158	1·0	−0·1	−0·5	−0·4
175	−0·1	1·8	−0·4	−0·7
171	3·1	−0·4	−0·8	−1·6
177	2·3	1·3	−1·3	−1·7
144	−0·9	−0·4	2·0	0·1
156	−0·9	−0·6	−0·4	1·0
170	−1·9	−0·3	2·5	0·9
178	−0·1	0·2	4·4	1·5

Perusal of Table 8 shows that fusions of species-groups with similar positive characterisations are possible—for example species groups 144, 170 and 178 all characterize positively site-group III. Such heuristic higher groupings do not conform to those of the dendrogram (Figure 5), and the possibility of another classificatory strategy for species was considered. The heuristic species-groupings were retained and those given in Table 8 fused as follows:

A = 158 + 171, positive characterization of site-group I
B = 3 + 175, positive characterization of site-group II
C = 144 + 170 + 178, positive characterization of site-group III
D = 185 + 156, positive characterization of site-group IV
E = 177, positive characterization of site-groups I and II
F = 189, positive characterization of site-groups III and IV.

CHARACTERISTICS OF SPECIES IN SPECIES-GROUPS

Within each species-group, species were arranged in order of grades of conformity (VH, H and M) as defined earlier. Within these grades they were further graded in 'importance'. Importance values were estimated, within the 97 species, as the summated site-centred cube-root contributions of a given species to the site-classification. Values ranged from 79·2 to −24·1 and were graded: H $>$ 10, M 10 to 0, L $<$ 0. Within the conformity-importance groups species were arranged in systematic order, with numbering as in the Appendix, and are given in Table 9.

INTERIM SUMMARY OF SPECIES-SITES ANALYSES

Site-group III, comprising two sites (11, 15) and with a sediment of fine sand with a low percentage of mud, has the richest characterizing biota. This comprises the 24 spp. of

TABLE 9

CHARACTERISTICS OF SPECIES-GROUPS (SITE-ANALYSIS).

Species Group	Conformity grade	Importance grade	Species numbers (see Appendix)
A	VH	L	80, 358
	H	L	85, 204, 244, 311, 359.
	M	H	197, 420
		L	55, 66, 67, 126, 149, 214, 296, 303.
B	VH	H	364
		M	374
		L	306
	H	M	165
		L	277
	M	H	263
		M	342
		L	18, 97, 160, 286, 309, 346.
C	VH	H	129, 139
		L	109, 131, 255, 279, 395, 402, 419.
	H	H	62
		M	283
		L	120, 125, 210, 299.
	M	M	97, 100
		L	171, 193, 199, 233, 253, 372, 393.
D	VH	H	385
		M	316, 382
		L	132
	H	H	75, 288, 350
		M	221
		L	54, 72, 107, 156, 184, 267, 381, 390
	M	H	330
		M	1, 145.
		L	69, 70, 134, 140, 308, 356, 359, 366, 415.
E	VH	H	37, 285
	H	L	270, 274
	M	H	90, 104.
F	VH	H	63, 289, 297, 394
	H	H	35, 340, 386
	M	H	123

species-group A and the eight of species-group F. It also has the highest number of uniquely characterizing species with VH conformity—nine. Against the figures of 32 and 9 for site-group III there follow: site-group IV (coarse sand)—28 and 4; site-group I (mud)—23 and 2; and site-group II (fine sand with higher percentage of mud)—19 and 3. The composition of the species-groups is considered later.

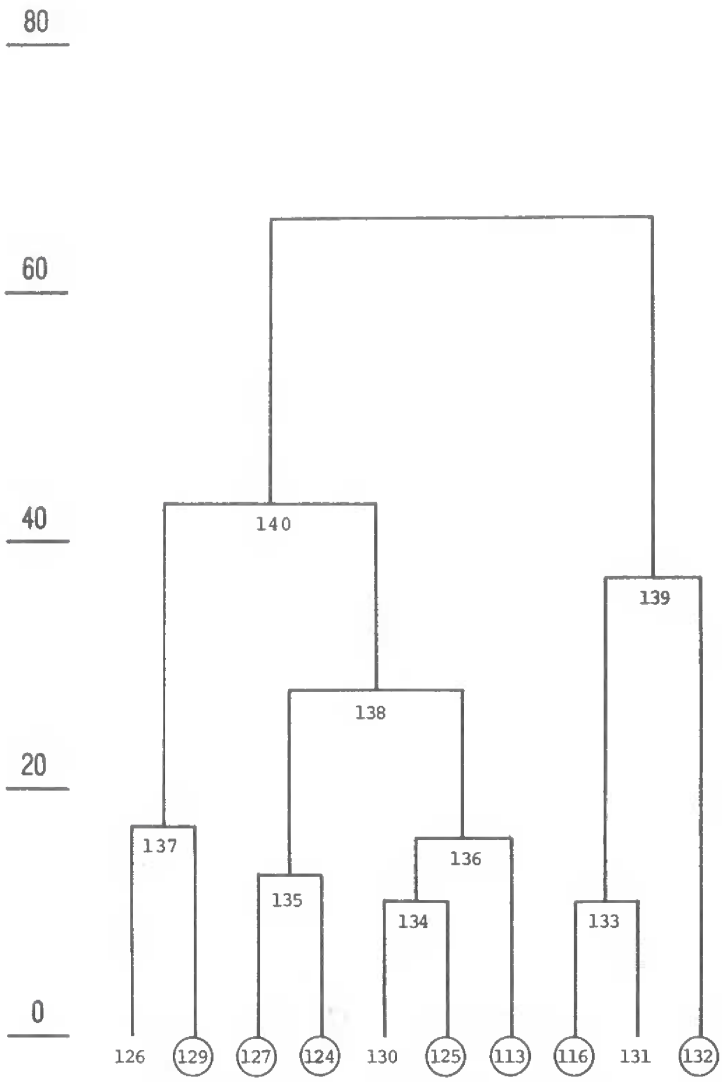

FIG. 6: Dendrogram of species classified by months. Species-groups with 'internal homogeneity' are ringed.

EXTENSIONS OF ANALYSES OF SPECIES-TIMES

Because the species-times relationships are of more interest than those of sites-times, expansion of times analyses were restricted to the former and now become a species × months × years situation in three dimensions.

RELATIVE IMPORTANCE OF EACH COMPARISON

Dealing with the original 71 species, mean variance per comparison is shown in Table 10. It will be noted that the total variance is half that of the species-times comparison listed in Table 7. The months × years comparison is approximately twice the importance of

TABLE 10

MEAN VARIANCES PER COMPARISON.

Nature of Comparison	Variance attributable to: months	years	species	interaction
Inter-months	—	0·270	0·077	0·055
Inter-years	0·270	—	0·129	0·055
Inter-species	0·077	0·129	—	0·055

the species × years, which in turn is almost double that of the species × months comparison. In other words, firstly changes in total populations with time are the most important elements and secondly that a monthly pattern of species common to the two years will be the 'weakest' of the three which emerge. This contrasts with the reasonable similarity of the month totals of species summated between the two years (see Table 5) and indicates that different species are replacing one another tolerably precisely from the months of 1970 to the equivalent months of 1971.

Seasonal and annual associations of species are investigated below, meanwhile the interaction values (0·055) should be noted. While low in absolute terms they are high relative to the species-months comparison. Again no ecological interpretation of this interaction is attempted.

SPECIES-MONTHS RELATIONSHIPS

Only four months (1, March; 2, June; 3, Sept.; and 4, Dec.) are involved. The months classification is of little interest, the dendrogram showing an initial dichotomy of 1+2 and 3+4. The similarity between 3 and 4 is slightly more than between 1 and 2.

The dendrogram of the species classification (Figure 6) was taken to the 10 group level, and the seven groups containing the species with the largest deviations of species-centred values were internally homogeneous in that all species characterized the same month in the same way. These groups are ringed in Figure 6. However the remaining three groups, which contained most of the species (46/71) each included species with either two or three types of month characterizations. This heterogeneity was not resolved by a finer classification. Even more so than in the study of species characterizing sites, was it necessary to alter the computer classification, and in the present case it was discarded.

Perusal of the values of species centred deviations showed, as with the species in site-groups, that some species had an outstanding positive deviation and hence positively characterized one of the four months. Others had negative characterizations and some appeared to have both positive and negative ones.

A method of quantifying an 'outstanding' deviation was required, bearing in mind that tests of significance are not possible with only four entities. That adopted was the proportion of the total variance of differences of the species-centred values contributed by the selected species-in-month values. Values for the 71 spp. ranged from ca. 0·3 to 0·76 and were graded arbitrarily as follows: 0·3–0·49, L (17 spp.); 0·50–0·59, M (21 spp.); 0·60–0·69, H (22 spp.); and 0·70–0·76, VH. Species with a L grade were eliminated.

When one of the remaining species appeared to characterize two seasons, one positively and the other negatively, it was accepted if (a) the variance due to these two seasons was 0·95 or more of the total, and (b) several such species showed similar characterizations. On these bases eight species with double characterizations were accepted.

It is appreciated that these criteria operate more stringently with respect to the month-groupings than those adopted for the site-groupings. This was done deliberately because in the present case there are not tests of significance and because there are fewer degrees of freedom.

TABLE 11

SPECIES, WITH NUMBERS FROM APPENDIX, WHICH CHARACTERIZE MONTHS.

Species group	Conformity grade	Importance grade	Species numbers
A	H	M	139
(+ve March)	M	H	123, 297
B	VH	L	165, 267
	H	H	73, 76
(+ve June)	M	M	385, 37
		L	360
C	VH	L	1, 373, 413
	H	M	29, 104
(+ve Sept.)		L	62, 100, 343, 367
	M	L	236, 241
D	H	L	145, 269, 306, 316
(+ve Dec.)	M	L	77, 283, 383
E	VH	H	289, 344
		M	387
	H	H	35, 364
(−ve March)		M	330, 420
		L	134, 263, 285, 342, 419
F	M	M	75
(−ve June)			
G	VH	L	221, 279
	H	L	288
(−ve Dec.)	M	H	90
		M	91
H*			
(−ve March)	H	H	63, 394
	M	H	36
		L	74, 204, 328
(+ve Sept.)	M	L	244, 341

*Double characterization −ve March, +ve Sept, grading restricted to outstanding cases.

Using these criteria and re-sorting the groups obtained by computer classification gave eight species groups. Conformity values of each species were obtained as previously—precise values differ because they were derived on different assemblages, one of 97 spp. and the other of 71. In Table 11 these data are given with the months they characterize positively, negatively and both.

Because only four months are considered and conformity grades are arbitrary the analysis was not extended beyond the 71 species of Table 6, and of the 54 species accepted 30 characterize months positively, 24 negatively, and 8 give double characterizations. The outstandingly 'weak' season is March with only three positive species and with 18 negative. It is followed by December with seven positive and five negative. The 'strongest' season is September with 19 positive and no negative species.

Species-Years Relationships

The interest is in species-groupings, and the computer classification dissects an array of numbers in which each species bears balancing positive and negative deviations in the species-centred values. Groups are tabulated below by positive characterizations, also listed are the range of deviations in each group, the number of species it contains and the arbitrary grades of conformity which were given. Because there is only a single degree of freedom these grades were applied stringently.

TABLE 12
Number of Species of Different Conformity Grades which Characterize Positively the Years 1970 and 1971.

1970		1971		Conformity grade
Range	No. spp.	Range	No. spp.	
0·44 – 1·1	10	0·0 – 0·7	11	discard
1·5 – 2·5	7	1·1 – 2·6	6	L
3·1 – 3·9	10	3·0 – 3·6	7	M
4·1 – 5·4	9	4·2 – 5·5	6	H
6·8 – 8·1	5	9·8	1	VH

Species are listed, with numbers from Appendix, in Table 13 for the upper three conformity grades, together with importance values obtained in the usual way.

Months-Years Relationships

Data are given as a double 2-way table in Table 14 and show that the 1971 biota is less than that of 1970, suggesting adverse effects of the flood. This conclusion is negatived by the data in Table 5 (second column) which deals with all species and not merely the 71 used for Table 13. The lowest value in Table 5 is for March 1970, before the flood; this is confirmed in Table 14.

TABLE 13
SPECIES, WITH NUMBERS FROM APPENDIX, WHICH CHARACTERIZE POSITIVELY THE YEARS 1970 AND 1971.

Species group	Conformity grade	Importance grade	Species numbers
A	VH	H	63, 344, 350, 364
		L	343
(+ve 1970)	H	H	73
		M	129, 159, 387
		L	37, 77, 360, 383, 390
	M	H	340, 394
		M	385
		L	1, 62, 204, 265, 279 285, 381
B	VH	L	342
(+ve 1971)	H	H	289
		M	104
		L	308, 341, 367
	M	H	35
		L	95, 145, 221, 236, 316, 382

TABLE 14
TWO-WAY TABLE OF MONTHS-YEARS; UPPER VALUES CENTRED BY YEARS, LOWER VALUES BY MONTHS. YEAR SUMMATIONS AT RIGHT, MONTHLY ONES BELOW.

		Months 1, March	2, June	3, Sept.	4, Dec.	Year Summations
Years	1, 1970	−0·5 −102·2	43·8 44·8	−1·3 43·0	25·7 14·3	y_1 67·7
	2, 1971	0·5 −67·3	−43·8 −9·0	1·3 79·5	−25·7 −3·2	y_2 −67·7
	Monthly Summations	m_1 −169·5	m_2 35·8	m_3 122·5	m_4 11·1	

CONSIDERATION OF SPECIES-GROUPINGS

GENERAL COMPARISONS OF GROUPINGS

There are two difficulties. The first is that the species-groups derived by the computer analyses did not precisely coincide with those required on conceptual grounds—it was by using the latter that groups were accepted. The second is that a test of conformity of species

to entity-groupings which had some statistical significance could only be applied to the species-in-sites data. This allowed acceptance of more species in sites data (97) than in months (54) or years (38) data.

A large fraction of the species which were above the M grade of conformity in the sites analyses were present in the other lists (39/97) and with lists of equal length the fraction would have increased. To exclude from site-classification all species with marked seasonal or annual patterns, as Petersen (1914) suggested, would greatly disturb the site-analyses and exclude much valuable data.

On general grounds one might have suspected that species of VH conformity to a particular entity group would include many cases of faithful species, which in turn would be uncommon and have low importance values. Survey of the data did not support this expectation; instead there are many cases of VH conformity coinciding with H importance. In these cases the diagnostic species are those of high dominance/constancy, and we have 'Petersen type communities' in the sense used in our previous paper (Stephenson, Williams and Cook, 1972). The difference is that these apply in an area sense (as did Petersen's) but also in a season and a year sense.

Post-Analytical Data Reduction

Ninety-seven species can be accommodated in the site-groups. For each we have data in continuous form on the degree of conformity to the site-groups and on relative importance over all sites. Data involving this sort of detail are difficult to comprehend so both conformity and importance values have already been graded. As in earlier work (Stephenson, Williams and Cook, 1972) further data compression is necessary for comprehension and below we eliminate all except those with VH conformity or H importance. These reduced data are given in Table 15 and are discussed below, comparable data for month-groups and year-groups are given in Tables 16 and 17.

Species in Site-Groups

Site-group I comprising the muddy sites is characterized uniquely by *Leocrates* (80) and *Ophiura kinbergi* (358) as VH conformity species and *Rhizopa* (197) and *Halophila spinulosa* (420) as H importance species. Ophiuroid 'communities' are known from muddy grounds from many parts of the world (see Thorson, 1957) and from our earlier work in Moreton Bay (Stephenson, Williams and Lance, 1970) and in New Guinea (Stephenson and Williams, 1971). This particular species has not been involved previously.

Site-group II comprising fine sand with a relatively high percentage of mud is characterized uniquely by three species at VH conformity levels. These are *Tellina lilium* (306), *Protankyra* sp. (364) and *Microcosmos* (374). The H importance species are *Ensiculus* (263) and *Protankyra* (364). Here the coincident occurrence of *Protankyra* indicates that a dominant species is characterizing a community in the classical manner (see Petersen, 1914: Stephenson, Williams and Cook, 1972). Community indicators, comparable to some of the present species, occur elsewhere, for example the many *Tellina* communities listed by Thorson (1957). The present species *T. lilium* has moderate constancy for a site-group which is predominantly muddy north of the mouth of the Brisbane River (Raphael and Stephenson 1972). In the present case it is, however also associated with *Protankyra*.

TABLE 15
SPECIES (IN GROUPS) CHARACTERIZING SITE-GROUPS* (CONDENSED FROM TABLE 9). POSITIVE CHARACTERIZATIONS.

Species group	Selected species VH conf.	H importance	Site-group characterized
A	80, 358	197, 420	I (sites 1, 2, 3, 5)—mud
B	306, 364, 374	263, 364	II (sites 4, 12, 14)—fine sand, high mud
C	109, 129, 131, 139, 255, 279, 395, 402, 419	62, 129, 139	III (sites 11, 15)—fine sand, low mud
D	132, 316, 382, 385	75, 288, 330, 350, 385	IV (sites 6, 7, 8, 9, 10, 13) —coarse sand
E	37, 285	37, 90, 104, 285	I and II
F	63, 289, 297, 394	35, 63, 123, 289, 297, 340, 386, 394	II and III

TABLE 16
SPECIES (IN GROUPS) CHARACTERIZING MONTHS-GROUPS* (CONDENSED FROM TABLE 11).

Species group	Selected species VH conf.	H importance	Month characterized
A	—	123, 297	March (+ve)
B	165, 267	73, 76	June (+ve)
C	1, 373, 413	—	Sept (+ve)
D	—	—	Dec (+ve)
E	289, 344	35, 364	March (−ve)
F	—	—	June (−ve)
G	221, 279	90	Dec (−ve)
H	—	63, 394	March (−ve), Sept (+ve)

*Only VH conformity and H importance species are listed. Species numbers are from the Appendix.

TABLE 17
SPECIES (IN GROUPS) CHARACTERIZING YEAR-GROUPS* (CONDENSED FROM TABLE 13).
POSITIVE CHARACTERIZATION.

Species group	Selected species VH conf.	H importance	Year
A	63, 343, 344, 350, 364	63, 73, 340, 344, 350, 364, 394	1970
B	342	35, 289	1971

*Only VH conformity and H importance species are listed. Species numbers are from the Appendix.

This latter species, under the name of *Leptosynapta* was one of the species which, in the earlier dredge survey (Stephenson, Williams and Lance, 1970) characterized the peripheries of the extensive sloping areas of mud to the north of the Brisbane River. In that earlier survey no '*Protankyra* grounds' were located in the Peel Island area. In the earlier survey *Ensiculus* was another characterizing species, but was not associated with the others now listed. It did characterize many of the areas near Peel Island, including the location of the present site-group.

Site-groups I and II are collectively characterized by two species of VH conformity—*Sthenelais* (37) and *Nucula astricta* (285), and four species of H importance—the two just cited together with *Nephtys* (90) and *Terebellides* (104). The three polychaetes have almost cosmopolitan distributions and have been involved in community descriptions elsewhere (see Thorson, 1957). Two (*Sthenelais* and *Terebellides*), like *Protankyra* in the dredge survey, characterized the muddy grounds to the north of the Brisbane River. Of these, one (*Terebellides*) is an important community indicator in the current work of Raphael and Stephenson. Again there is evidence of a 'Petersen-type community'in the co-occurrence of *Sthenelais* and *Nucula astricta* under both conformity and importance headings.

Site-group III comprising fine sand with a relatively low percentage of mud is uniquely characterized by nine species of VH conformity: sabellid 4 (109), the polyspecific *Euclymene* spp. (129), *Isolda* (131), *Petaloproctus* (139), *Circe* (255), *Malleus* (279), *Acetabularia* (395), *Gracilaria verrucosa* (402) and *Halophila ovalis* (419). Of these *Euclymene* and *Petaloproctus* are of H importance, as is anothèr species *Eunice antennata* (62). Many of these species also characterized site-groups in our dredge survey but were spread between several species groups and there is little correspondence. None of the species characterize the areas being studied by Raphael and Stephenson.

Site-group IV comprising coarse sand is uniquely characterized by four species of VH conformity: *Lygdamis* (132), *Tucetilla* (316), *Molgula rima* (382), and *Polycarpa fungiformis* (385). The H importance species are *Glycera americana* (75), *Paphia gallus* (288), *Thermiste* sp. (330) and *Polycarpa fungiformis* (385). Again several species are common to one or another of the species-groups derived in the dredge survey, and none are amongst the important species just north of the Brisbane River (Raphael and Stephenson 1972).

There remain several species (species-group F) characterizing site-groups II and III. The VH conformity species are: *Eunice* cf. *indica* (63), *Paphia subrugata* (289), *Placamen tiara* (297) and *Branchiostoma* (394). All four have H importance values as have ?*Euleanira* (35), *Chaetopterus* (123), *Amphioplus depressus* (340) and *Polycarpa pedunculata* (386). Again most occurred in one or another of the groups from the dredge survey, but on preliminary results few appear important just north of the Brisbane river.

Summarizing the species in sites analysis: (a) there are several cases of 'Petersen-type communities' in which species of VH conformity also have H importance values, (b) many of the characterizing species of the present survey also characterized site-groups in the earlier dredge survey (Stephenson, Williams and Lance, 1970) but there are only slight correspondences in detail, (c) several of the species characterizing the more muddy sites of the present survey also in the current work, are characterizing muddy sites just north of the Brisbane river.

Several species which were intuitively thought to be characteristic of one area or another are not listed above. They include *Discobotellina* (1) which only has M conformity to site-group IV. Several species which occurred commonly and which might characterize the total area of investigation rather than sections of it are not listed. One such is *Leanira* (36), which did not conform to the major site pattern.

Species in Month-Groups

March has no species with VH positive conformity but two with H importance: *Chaetopterus* (123) and *Placamen tiara* (297). It is negatively characterized at the VH conformity level by *Paphia subrugata* (289) and *Amphiura catephes* (344), and at the H importance level by ?*Euleanira* (35) and *Protankyra* (364). Additional species are considered below.

June only has positive characterization at the levels now considered; the VH conformity species are *Callianassa* (165) and *Gari venta* (267) while the H conformity ones are *Chloeia* (73) and *Glycera prashadi* (76). September again only has positive characteristics with three species of VH conformity and none of H importance. The former are *Discobotellina* (1), *Eugyra* (373), and *Pseudocodium* (413). Additional species are considered later. December has no positive characterizations at the prescribed levels and is negatively characterized at VH conformity by *Herpetopoma* (221) and *Malleus* (279) and at H importance by *Nephtys* (90).

Finally, two species characterize March negatively and September positively at H importance; they are *Eunice* cf. *indica* (63) and *Branchiostoma* (394).

The results show only tenuous resemblance to the preliminary conclusions on seasonality from the earlier dredging work. In both studies *Protankyra* negatively characterized the warmer part of the year. In the previous work *Discobotellina* showed no seasonality, but now it does. This may relate to the different areas of sampling because the species is uniformly present in large numbers in the northern part of Moreton Bay but appears to occur in a patchy and spasmodic fashion near Peel Island. Studies by Stephenson and Rees (1965a, b) indicate that its normal life-span exceeds a year.

There are perplexing aspects to the results. One would have expected the seasonal species to be predominantly small, to include many algae and, following Kott's (1972)

interpretation of our incomplete tunicate collections, to include many tunicates. In fact the species listed earlier include many of the larger forms, for example *Chaetopterus*, *Placamen tiara*, *Paphia subrugata*, *Chloeia* and *Malleus*. Moreover none of the above are highly mobile with the possibility of movement into and out of the area. This is the likely explanation of the seasonality of *Callianassa* which here occurs as juveniles and in which adults are likely to be more than one year old (Hailstone and Stephenson, 1961).

A possible explanation of this paradox is in the existence of topographical micro-patterns with accidental concentration of sampling on certain patterns in certain seasons. As indicated elsewhere much more frequent sampling is required for adequate investigation of seasonality. Studies of populations of individual species which involve size measurements are also required; to date these have only done on *Discobotellina* (Stephenson and Rees, 1965a, b) and on intertidal populations of *Callianassa* (Hailstone and Stephenson, 1961).

Species in Year-Groups

The five species with VH conformity for 1970 are: *Eunice* cf. *antennata* (63), *Amphiura bidentata* (343), *A. catephes* (344), *Ophiacantha* (350) and *Protankyra* (364). Of these *Eunice*, *A. catephes*, *Ophiacantha* and *Protankyra* have H importance, as have *Chloeia* (73), *Amphioplus depressus* (340) and *Branchiostoma* (394). A single species characterizes 1971 with VH conformity—*Amphioplus* sp. (342) with two species of H importance—?*Euleanira* sp. (35) and *Paphia subrugata* (289). With the exceptions of *Chloeia* and *Paphia* all are small species and many are surface-dwelling ophiuroids whose populations might be expected to change from year to year. The surprising exclusions from the list are the smaller tunicates—these were below the arbitrary levels which were selected.

DISCUSSION

Introductory

The objective of the present work was to investigate a suspectedly complex benthic biota and to attempt to resolve the complexity into a number of patterns in terms of area and of time. We use the term 'complexity' in deliberate avoidance of 'diversity' which means so many things to so many people.

Fifteen stations were sampled in quintuplicate at each of four seasons for two years. The method of analysis with which we began was developed by use of a selected array of the present data, has already been described (Williams and Stephenson, 1973), and has been discussed earlier in the present paper. It involves three arbitrary elements. The first is the stringency of transformation (we used cube roots), the second the level of data reduction (this we modified, excluding initially species contributing less than 0·5% of the variance to the two initial analyses), and the third the sorting strategy (we used flexible).

Site-Groups

We first examined the site-groupings obtained using species as attributes (summed over all times). The past literature on soft-bottom benthos has sometimes stressed site-groupings and sometimes species-groupings, and there is uncertainty amongst ecologists generally as to which are the most important. Noy-Meir's (1970) canvassing of opinion of non-marine ecologists suggested a preference for site-groups. If, following Dahl (1908),

communities are delimited biotopically, a view which appears (unforunately) to be gaining ascendency in ecological texts (see Stephenson, 1973), then clearly site-groups are at the core of the community concept. While we later concentrate on species-groupings, site-groupings are of great importance for two reasons. The first is that we can use their extrinsic abiotic attributes as criteria for choosing between classificatory methodologies (see Stephenson, Williams and Lance, 1970; Stephenson and Williams, 1971; Stephenson, 1973). The second is that we can use site-groups via two-way coincidence tables to link the species-groups to the abiotic environmental features.

We used the first in preliminaries to the present work and compared the site-groups which were generated by different transformations of three sub-sets of the present data. It was on this basis that a cube-root transformation was selected.

As regards the second, there is an extraordinary resemblance between the site-groups generated by using species as attributes and the sediment classification of the sites. The correspondence is so close that the effects of other abiotic variables are completely masked. This almost exact relationship was not apparent when date for our earlier paper (Williams and Stephenson, 1973) were at hand. Sediment data for this earlier work were obtained at the start of the survey (March 1970), the data used in the present work was the average of values for March 1970 and December 1971.

The differences between these two sets of values were greater than expected, and because sediment grades are so important it is evident that much more data should have been collected. This would have indicated whether sediments were changing on a short term basis (for example between spring and neap tides), on a long term basis (over several years) or whether the differences in the sets of data are due to different 'random' samplings of topographical micropatterns.

An original objective was to determine whether there were small scale area patterns in the area. They are clearly present. Within one area (I) of 0·24 km^2 there is one site-group and part of a second, and within another (area III) of 0·36 km^2 there are elements of three site-groups. Within our area it would have been desirable for the intersite distances to have been no greater than 0·25 km for adequate delineration of the kind of group we obtained. This indicates that close spacing is likely to be desirable in inshore sub-tropical areas with varying sediments and under some estuarine influences. Pearson (1970) has already suggested that the scale of inshore patterns is finer than offshore. We have already indicated (Stephenson, Williams and Cook, 1972) that Petersen's (1914) stations were too distantly spaced to show coherent area patterns, and the present work confirms this opinion.

A second kind of site-grouping was provided by the analyses—this is using times as attributes (with summation of species). It gives little conceptual advantage over consideration of the summed values of all species over all times in the sites—as in Table 5. The main conclusion is that the muddy sites (1, 2, 3 and 5) have the lowest total populations.

Species in Sites

As the present work progressed it became evident that interest was primarily focussed on species. It was equally evident that the 'inverse' classifications as revealed in the dendrograms were not producing optimal sense. This led to the first important modification of

the Williams and Stephenson (1973) methodology. In the previous paper in order to produce a single two-way table showing site-groups and their constituents and species-groups with their constituents, we had to marry classifications using two different sets of derived data. These were site-centred deviations as used in the site classification and species-centred deviations as used in the species classification. We did this, in tables designated 'B', by taking the mean of the two differently centred values. In an attempt to resolve some of the problems of species classification we considered only species-centred values. This gave slightly greater conceptual sense, but difficulties remained. Their resolution, such as it was, was affected by concentrating on the species-centred values in site-groups obtained by using site-centred data.

The computer classification we used is based upon the euclidean distances of species one from another (using cube-root data) and these distances are greater with the more abundant species. The less abundant species tend to be 'lumped' into what are virtually discard groups.

The conceptual aim in a species/site situation is to determine which species characterize a site by predominantly occurring there (or by predominantly not occurring there). This predominance is not necessarily proportional to the abundances of the species, indeed on the assumption that species of high fidelity are relatively uncommon, the reverse might be expected.

In the species-in-sites classification, species-groups derived by variance of differences were acceptable at different levels on the dendrogram, and only at lower levels for the less common species. It was necessary to redesign the upper parts of the hierarchy by commonsense methods.

Neither the original strategy nor its commonsense substitute were satisfactory for deciding in doubtful cases whether a species was predominant in a particular site-group. Here a 'test of significance' was used—the ratio of between site-group variances to within site-group variances (the F test). The affinities between species on different branches of the dendrogram became obvious when this ratio was employed.

The availability of an approximate test of significance of a given species to a predetermined site-grouping is an important auxillary advantage of the present methodology. It allowed us to reject species of low conformity to the grouping, and also to scan the total species list (beyond those with high site variance values) to pick out further conformers. As a result almost one quarter of the biota are known to conform to the site-groups we had specified.

Having selected some species with high contributions to site-variance which did not conform to the original site-groupings we added species lower on the site-variance list and searched for an alternative site-grouping. None eventuated in the present case. There is no certainty that this would be so in other situations and it is quite possible that an area might contain sediment-sensitive and pollution-sensitive species which could generate alternative site-groupings. To be able to explore such possibilities is another advantage of the present technique.

The tests of significance were used to produce grades of conformity of species to site-groups, and we have used the term 'conformity' throughout. In our previous numerical analyses of benthic data we have characterized species by the terms long used by terrestrial

botanists—dominance, constancy and fidelity. Previously the stress has been on dominance and constancy (see Williams, Stephenson and Lance, 1970; Stephenson and Williams, 1971; Stephenson, Williams and Cook, 1972). 'Conformity' combines the three concepts. Thus high positive conformity of a species to a site-group means that most individuals occur in that group. This is irrespective of the actual numbers there present. High positive conformity can occur with an uncommon species, in which case it equates to fidelity. It can also occur in an abundant species, in which case it is likely to equate to dominance/constancy. Another type of conformity occurs, although more obvious in later analyses. This is high negative conformity—it means that a species 'avoids' a site-group. To describe this in terms of negative dominance/constancy/fidelity introduces conceptual problems, so throughout we adhere to the terminology and concept of 'conformity'.

While dominance grades in a given site-group are thus discarded, relative abundances of species in a particular data matrix are readily obtained. They are the summations between site-groups of the site-centred deviations which are used in site-grouping. Because the term 'dominance' has a within site-group connotation we have used the term 'importance' for these summated values and graded them on an arbitrary basis. We might expect that the less common species with lower importance values would have the most discrete sorting into site-groups (i.e. show the highest fidelity) but the data did not show this—neither did it apply to the species in month-groups detailed later.

Times Analyses

The relative importance of times and sites with respect to species is indicated in Table 7 and is about 2:3. The times-sites comparison is a measure of the changes in total population (all species summated) and is less than that of species-times in the ratio of 4:5. The chronological changes in total population through time are also shown in Table 5.

Attempts to classify times by species were regarded as unsatisfactory because the dimension time involves two dimensions—months and years. The time-species data were expanded to three dimensions of species $\times$ months $\times$ years. This gives, overall, a partial partitioning in four dimensions. In general terms by successive paritioning of a matrix in which one dimension is species, there is no theoretical limit to the number of dimensions which may be explored.

Within the species-times data, Table 10 shows that the greatest amount of variance is between months and years—i.e. in total population of all species summated, rather than in either of the combinations involving species. This indicates considerable replacement of one set of species by another set (or sets) as time proceeds. The species-year variance is almost double that of species-seasons indicating that annual changes in species composition are more important than seasonal ones.

Data on the population changes from 1970 to 1971 are ambiguous (compare Tables 5 and 14) but it is clear that if there was any population reduction due to floods, there was a delay period of about six months, as evidenced the low values of June 1971. The smallest total population was in March 1970; then and previously there had been no obvious abiotic adversities. The highest total population was in September 1971 and because this followed an exceptionally dry winter, it may indicate that the salinities in the area are sub-optimal throughout. In summary explanations of differences in populations between 1970 änd 1971 are tenuous.

Analyses of the species-months data were concentrated on delimiting species-groups characterizing particular months. Because there are only four months to consider, tests of significance of conformity could not be made. It is plain that, for a satisfactory study of season changes more frequent sampling, for example 12 times annually, is required. We estimated conformity by using ratios of variance and obtained arbitrary grades; because they were arbitrary we did not extend the selection to species beyond the 71 species list of Table 6. Seventeen of the 71 species were eliminated because of very low conformity, and the remaining 54 already present more data than is readily comprehensible. Values of importance for the 54 species were obtained and have been cited (Table 13).

The main difference in emphasis between the site-conforming species and the month-conforming species is that the latter contained a large fraction (24/54) giving negative characterization—almost exclusively of March.

Analyses of species/years were purely in terms of species, and grades of conformity are arbitrary. They were made by using the points of dissection in an essentially continuous array which were revealed by the classificatory programme. The flexible sorting strategy which was used here proved its value—it optimizes discontinuties. Again the inadequacy of the data are apparent. Because annual effects are clearly important (in the present case more important than seasonal ones), to document their reality in terms of significance and to elucidate their causes would require data extending over possibly a decade.

With the present data limitations each species which positively characterizes one year gives an equal negative characterization of the other. Comparisons of the numbers of positive and negative characterizations with those of other analyses are impossible.

The most important general comment on the species-times data is that it allows us to think of species-groups in seasons and species-groups in years as well as species-groups in sites. We are no longer like Petersen (1914) bound to eliminate 'seasonal animals' from our ideas of communities, or more strictly of associations (Mills, 1969; Stephenson, Williams and Cook, 1972). We return later to the contribution of these three kinds of species-groups to an understanding of the complexity of the area.

The most important pragmatic consideration is that if a sampling programme is limited to a single set of samples taken 'instantaneously', a great deal of relevant information is likely to be missing. We understand that such sampling programmes are normally all that are required by authorities considering whether or not an engineering project is likely adversely to effect an environment—these are the 'environmental impact' statements. It would clearly be impossible, even with the present fairly extensive data, for us to predict in any detail the natural changes which might occur in our sampled area. To predict with any degree of confidence, the possible effects of superimposed changes might require an initial survey of ten years duration.

Complexity and Diversity

In the extensive literature upon diversity which has developed since the later 1950's considerable attention has been paid to the comparison of diversities from different situations, and particularly from different latitudes. Recent reviews have been given by Recher (1972) and by Whittaker (1972) and critical earlier papers are by Fischer (1960), Klopfer and MacArthur (1969), Saunders (1968) and Thorson (1952). At the level of

species richness there is an immense literature in faunistic and floristic treatments of various taxa.

There seems to be general agreement that diversity comparisons should either be within ecological units or between them. The units envisioned are sometimes habitats, and thus we have within-habitat α diversity and between-habitat β diversity. Sometimes diversity is considered within an 'ecological community' (Edden, 1971) and sometimes applying to a 'community biota' (Hendrickson and Ehrlich, 1971). The concepts and comparisons are valid when, and only when, there is agreement on what a habitat is or an ecosystem is. Delimitations of 'habitats' and 'ecosystems' involves human judgements which seem often to be made upon undefined bases. We suspect that a 'habitat' judgement is usually made by the human eyes or by instrumental measurements of the abiotic features in a situation. If so it is directly comparable to biotopic concepts of the community which originated with Dahl (1908). These notions seem open to severe criticism in that we determine the boundaries and hope that the organisms will respect them. The history of marine soft-bottom 'communities' which began with Petersen (1914) has not a tradition of accepting biotopic boundaries, probably because consideration of abiotic attributes produces continua. Boundaries have been set by the organisms, the 'communities' are biocoenoses. In fact as already stated by Mills (1969) and Stephenson, Williams and Cook (1972) the word 'associations' is more appropriate.

If the 'communities' are though of as site-groups derived by using species as attributes, if there is a complex situation and if one is not to discard data on most of the species, one is forced into one or another method of numerical classification using computer techniques. Different methodologies produce different groupings and techniques of handling data are still evolving. Some advances were made in the preliminary paper using some of the present data (Williams and Stephenson, 1973) and others are contained in the present paper. No satisfactory technique exists in which there are statistically acceptable tests of the level at which, in a classificatory hierarchy, a site-group can be accepted or rejected.

In comparisons between apparently similar 'habitats' at different latitudes it is possible that the sizes of site-groups which one would accept would differ. In more specific terms one explanation for increased tropical diversity could be the existence of topographical micropatterns of site-groups. Another term for this is 'patchiness', and references to this are given by Pielou (1966) and Lloyd (1967). Both deal with the topic somewhat theoretically. In studies of soft-bottom benthos there appear to have been no investigations of the scales of patterning in comparable tropical, subtropical and temperate soft bottom environments. We believe our own investigations have been of a finer scale than others and we have revealed small-scale topographical patterning. We suspect that the real scale may be finer than that which we have revealed.

Meanwhile, as Pearson (1970) has indicated, there may be obvious geographical change in patterning as one moves from inshore to offshore localities. This, as well as latitudinal changes, merits detailed investigation.

There are many problems centred around the time factor in ecological surveys, including the methodological problems with which we have been concerned earlier in this paper. There are also conceptual problems, for example whether or not the 'community concept' should or should not include chronological changes. Many of the earlier

definitions of communities and associations exclude the time element deliberately or by implication. As stated in an earlier paper (Stephenson, 1973): 'For example Möbius (1877) spoke of a community in which the total of species is mutually linked under the *average external conditions of life*. Hesse (1924) said that the groupings correspond with *average prevailing conditions* [The italics are not in the originals] . . . It seems that the terrestrial botanists have adopted a similar view. Thèir associations are characterized by such things as constancy of species, and seasonal species are clearly inconstant on a continuous chronological scale'. Later definitions involve dynamic concepts, for example Resvoy's (1924) mention of dynamic balance, and Emerson's (1939) concept of a chronologically adjusting super-organism.

Once the notion is established that there are seasonal changes and 'seasonal communities' we are in danger of conflict with one of the shibboleths of current thinking about diversity. This is the belief that high diversity occurs in situations of high stability. This danger of confrontation cannot be avoided if there is a component of complexity which is due to different annual 'communities', in which there is no evidence of regularity of re-occurrence. We have demonstrated that there are differences between one year and another in our own situation and that they are more important than seasonal differences.

There is nothing intrinsically wrong with the argument that a situation showing annual instability should be more complex than one with annual stability. Indeed the argument appears as if it should run: biotic uncertainty equates to abiotic uncertainty; whence diversity equates to an environment showing differences from year to year. To this argument we should add two important riders.

The first is that, in our present situation, there is no clear evidence that the difference between the two years of the investigation was directly due to abiotic events. The second is that in discussing chronological instability in abiotic factors there are likely to be differences in scale. Gross instability is likely to lead to reduction in complexity, whereas instability within 'acceptable limits' may well increase it. The 'acceptable limits' will be in terms of the range and availability of organisms capable of immediate replacements in changed areas. What applies to an inshore situation with occasional reduction of salinities, or with changes in sedimentary patterns, can not be expected to apply to the terrestrial biota of an oceanic island devastated by a volcanic eruption.

Just after the above was written the senior author was given by W. Sakai (private communication) results of a startling simple demonstration of the effects of instability within 'acceptable limits' causing an increase in diversity. Sakai worked on clumps of mussels and showed that moderate mechanical disturbance increased diversity.

ACKNOWLEDGEMENTS

We are deeply grateful to the following for identifications in the groups stated. Without this massive assistance species would have been confused or eliminated: Dr P. E. Gibbs (Marine Biological Lab., Plymouth, U.K.): Polychaetes—Amphinomids, Nereids, Glycerids, Opheliids, Orbinids; Mrs K. Hicks (Zoology Dept., University of Canterbury, N.Z.): Polychaetes—Lumbrinerids; Dr P. Hutchings (Australian Museum): Polychaetes—Terebellids, Ampharetids; Dr R. B. Spies (Dept. of Fisheries & Wildlife, Melbourne): Polychaetes—Flabelligerids; Mr B. M. Campbell (Queensland Museum): Crustacea—

general; Mr C. R. Smalley (Zoology Dept, University of Western Australia): Crustacea—Alpheids; Mr M. Johnston (Zoology Dept, University of Queensland): Crustacea—Cumacea; Dr D. F. Boesch (Virginia Institute of Marine Science, U.S.A.): Crustacea—Tanaidacea; Mrs H. King (Queensland Museum), Dr R. B. Wilson and Mrs S. M. Slack-Smith (Western Australian Museum), Dr W. F. Ponder (Australian Museum): Mollusca—Gastropods, Bivalvia; Mr W. A. Green (4/11 Wilson Street, Berwick, Victoria): Sipunculids; Dr A. N. Baker (Dominion Museum, N.Z.): Echinoderms—Ophiuroidae, Echinoidea; Dr D. L. Pawson (Smithsonian Institution, U.S.A.): Echinoderms—Holothurioidea; Dr P. Mather (Zoology Dept, University of Queensland): Tunicates; Mr O. E. S. Kelly (Zoology Dept, University of Queensland): Cephalochordata; Dr A. B. Cribb (Botany Dept, University of Queensland): Algae, Angiosperms.

We are also grateful to Mr W. Sakai (Dept of Biological Sciences, University of California, Los Angeles) for permission to quote from results of his current experiments.

APPENDIX I

Species Obtained, with Original Arbitrary Numbers.

PROTOZOA

FORAMINIFERA

1 *Discobotellina biperforata* Collins

PORIFERA

2 Cushion Sponge
3 Sponge 1
4 Sponge 2
5 Sponge 3
6 Sponge 4
7 Sponge 5
8 Sponge 6
9 Sponge 7
10 Sponge 8
11 Sponge 9
12 Sponge 10
13 Sponge 11

CNIDARIA, ANTHOZOA

GORGONACEA

14 'Whip coral'
15 'Rusty wire' gorgonid

PENNATULACEA

16 *Scleroblemnon* sp.
17 Sea pen

CERIATHARIA

18 cf. *Cerianthus* sp.

ZOANTHARIA

19 *Sphenopus marsupialis* (Gmelin)

ACTINIARIA

20 *Edwardsia* sp.
21 Anemone 1
22 Anemone 2
23 Anemone 3

PLATYHELMINTHES

POLYCLADIDA

24 Sp. 1
25 Sp. 2

NEMERTEA

26 'Black'
27 'Brown'
28 'Pale'
29 'Pink'
30 'Speckled'
31 'Sunburnt'
32 'White striped'
33 'Red'
34 'Red and white'

ANNELIDA, POLYCHAETA

APHRODITIDAE

35 ? *Euleanira* sp.
36 *Leanira yhleni* Malmgren
37 *Sthenelais boa* (Johnston)
38 Sigalionid 1
39 Sigalionid 2
40 'Small aphroditid' 1
41 'Small aphroditid' 2
42 'Small aphroditid' 3
43 'Small aphroditid' 4
44 'Small aphroditid' 5
45 'Small aphroditid' 6
46 'Small aphroditid' 7
47 'Small aphroditid' 8
48 'Small aphroditid' 9
49 'Small aphroditid' 10
50 'Small aphroditid' 11
51 'Small aphroditid' 12
52 'Small aphroditid' 13

NEREIDAE

53 *Ceratocephala sibogae* (Horst)
54 *Nereis jacksoni* Kinberg
55 *Leonnates stephensoni* Rullier
56 *Platynereis insolita* Gravier
57 *Websterineris punctata* (Wesenberg-Lund)

EUNICIDAE

58 *Arabella iricolor* (Montagu)
59 *Drilonereis* sp. 1
60 *Driloenreis* sp. 2
61 *Drilonereis* sp. 3
62 *Eunice antennata* (Savigny)
63 *Eunice* cf. *indica* Kinberg
64 Eunicid ('4 antennae')
65 *Lumbrineris latreilli* Audouin and Milne Edwards
66 *L. maxillosa* (Ehlers)
67 *L. mirabilis* (Kinberg)

68 *L. mucronata* Ehlers
69 *Marphysa sanguinea* Montague
70 *Onuphis* sp. ('long gill')
71 *Onuphis* sp. ('short gill')
72 *Rhamphobranchium* sp.

Remaining Errantia
73 *Chloeia flava* (Pallas) (Amphinomidae)
74 *Eurythoe cf. parvecarunculata* Horst (Amphinomidae)
75 *Glycera americana* Leidy (Glyceridae)
76 *G. prashadi* Fauvel (Glyceridae)
77 *Goniada eremita* Audouin and Milne Edwards (Glyceridae)
78 Hesionid 1 (Hesionidae)
79 Hesionid 2 (Hesionidae)
80 *Leocrates cf. claparedii* (Costa) (Hesionidae)
81 Phyllodocid 1 (Phyllodocidae)
82 Phyllodocid 2 (Phyllodocidae)
83 Phyllodocid 3 (Phyllodocidae)
84 Pilargid 1 (Pilargidae)
85 Pilargid 2 (Pilargidae)
86 Pilargid 3 (Pilargidae)
87 Syllid 1 (Syllidae)
88 Syllid 2 (Syllidae)
89 Syllid 3 (Syllidae)
90 *Nephtys dibranchis* Grube (Nephtyidae)

Terebellidae
91 *Amaeana trilobata* (Sars)
92 *Amphitrite rubra* (Risso)
93 *Lanice conchilega* (Pallas)
94 *Loimia ingens* (Grube)
95 *L. medusa* (Savigny)
96 *Lysilla* sp.
97 *Pista typha* Grube
98 *Pista* sp. 1
99 *Pista* sp. 2
100 *Pista* sp. 3
101 *Streblosoma gracile* Caullery
102 *Streblosoma* sp.
103 *Telothelepus* sp.
104 *Terebellides stroemi* Sars
105 *Trichobranchus gracialis* Malmgren

Sabellidae
106 Sabellid 1
107 Sabellid 2
108 Sabellid 3
109 Sabellid 4
110 Sabellid 5
111 Sabellid 6
112 Sabellid 7
113 Sabellid 8
114 Sabellid 9
115 Sabellid 10
116 Sabellid 11

REMAINING SEDENTARIA

117 *Amphicteis gunneri* (Sars) (Ampharetidae)
118 *Anchenoplax* sp. (Ampharetidae)
119 *Armandia cf. intermedia* Fauvel (Opheliidae)
120 *Armandia* sp. (Opheliidae)
121 *Bucherta* sp. (Capitellidae)
122 Capitellid 1 (Capitellidae)
123 *Chaetopterus variopedatus* Renier (Chaetopteridae)
124 *Cirriformia ankylochaeta* (Schmarda) Cirratulidae)
125 *Coppingeria longisetosa* Haswell (Flabelligeridae)
126 *Dasybranchus caducus* (Grube) (Capitellidae)
127 *Diplocirrus* cf *capensis* Day (Flabelligeridae)
128 *Diplocirrus* sp. 2 (Flabelligeridae)
129 *Euclymene* spp. (Maldanidae)
130 *Haploscoloplos bifurcatus* Hartman (Orbiniidae)
131 *Isolda pulchella* Muller (Ampharetidae)
132 *Lygdamis cf. indicus* Kinberg (Sabellariidae)
133 *Magelona cincta* Ehlers (Magelonidae)
134 *Magelona* sp. (Magelonidae)
135 Maldanid ('parchment-grit tube') (Maldanidae)
136 *Mesochaetopterus minutus* Potts (Chaetopteridae)
137 *Notomastus giganteus* Moore (Capitellidae)
138 *Pectinaria antipoda* Schmarda (Pectinariidae)
139 *Petaloproctus terricola* Quatrefages (Maldanidae)
140 *Piromis cf. arenosus* Kinberg (Flabelligeridae)
141 *Piromis* sp. 2 (Flabelligeridae)
142 *Polydora* sp. (Spionidae)
143 *Polyophthalmus pictus* Dujardin (Opheliidae)
144 *Pseudocapitella* sp. (Capitellidae)
145 *Spiophanes* sp. (Spionidae)
146 Spionid 1 (Spionidae)
147 Spionid 2 (Spionidae)
148 Spionid 3 (Spionidae)
149 *Sternaspis scutata* (Renier) (Sternaspidae)

UNCERTAIN FAMILIES

150 Polychaete 1
151 Polychaete 2
152 Polychaete 3

ARTHROPODA, CRUSTACEA

STOMATOPODA

153 *Squilla anomala* Tweedie
154 *S. fasciata* de Haan

DECAPODA

155 *Achaeus brevirostris* (Haswell) (Majidae)
156 *A. lacertosus* Stimpson (Majidae)
157 *Actaea savignyi* (H. Milne Edwards) (Xanthidae)
158 *Actumnus* sp. (Xanthidae)
159 *Alpheus distinguentus* de Man (Alpheidae)
160 *A. stephensoni* Banner and Smalley (Alpheidae)
161 *Alpheus* sp. near *pacificus* (Alpheidae)
162 *Alpheus* sp. 1 (Alpheidae)
163 *Alpheus* sp. 2 (Alpheidae)

164 *Axius glyptocercus* von Marthens (Axiidae)
165 *Callianassa australiensis* Dana (Callianassidae)
166 *Calmania prima* Laurie (Xanthidae)
167 *Ceratoplax truncatifrons* Rathbun (Goneplacidae)
168 *Chlorinoides longispinus* (de Haan) (Majidae)
169 *Cryptodromia unilobata* Campbell and Stephenson (Dromiidae)
170 *Cryptopodia queenslandi* Rathbun (Parthenopidae)
171 *Dorippe australiensis* Miers (Dorippidae)
172 ? *Globopilumnus* sp. (Xanthidae)
173 'Hermit crab' (Paguridae)
174 *Hexapus granuliferus* Campbell and Stephenson (Goneplacidae)
175 *Hyastenus convexus* Miers (Majidae)
176 *H. diacanthus* (de Haan) (Majidae)
177 *Leucosia ocellata* Bell (Leucosidae)
178 *L. pubescens* Miers (Leucosidae)
179 *Leucosia* sp. (Leucosidae)
180 *Libystes paucidentatus* Stephenson and Campbell (Portunidae)
181 *Macrophthalmus* sp. (Ocypodidae)
182 *Myra affinis* Bell (Leucosidae)
183 *M. australis* Haswell (Leucosidae)
184 *Nursia plicata sinuata* Miers (Leucosidae)
185 *Parthenope harpax* (Adams and White) (Parthenopidae)
186 *Parthenope* sp. (Parthenopidae)
187 *Phalangipus australiensis* Rathbun (Majidae)
188 *Pilumnoplax* sp. (Goneplacidae)
189 *Pilumnus contrarius* Rathbun (Xanthidae)
190 *P. minutus* de Haan (Xanthidae)
191 *Pilumnus* sp. (Xanthidae)
192 *Pinnotheres spinidactylus* Gordon (Pinnotheridae)
193 *Pisidia dispar* (Stimpson) (Porcellanidae)
194 *P.* cf. *spinulifrons* (Miers) (Porcellanidae)
195 *Polyonyx transversus* (Haswell) (Porcellanidae)
196 *Raphidopus ciliatus* Stimpson (Porcellanidae)
197 *Rhizopa gracilipes* Stimpson (Goneplacidae)
198 *Scyllarus sordidus* (Stimpson) (Scyllaridae)
199 *Thalamita sima* H. Milne Edwards (Portunidae)
200 *Typhlocarcinops decrescens* Rathbun (Goneplacidae)
201 *T. tonsurata* Griffin and Campbell (Goneplacidae)
202 *Xenophthalmoides dolichophallus* Tesch (Goneplacidae)
203 *Xenophthalmus pinnotheroides* White (Pinnotheridae)

Remaining Crustacea

204 *Whiteleggia stephensoni* Boesch (Tanaidacea)
205 *Cyclaspis* sp. 1 (Cumacea)
206 *Cyclaspis* sp. 2 (Cumacea)
207 *Heterotanais* sp. (Tanaidacea)
208 *Pomacuma australiae* (Zimmer) (Cumacea)

Mollusca

Gastropoda

209 *Adamnestia thetidis* (Hedley) (Scaphandridae)
210 *Bedeva hanlyi* Angas (Muridae)
211 *Cancellophora amasea* Iredale (Cancellariidae)
212 *Cerithiopsis (Notoseila) crotea* Angas (Cerithiopsidae)

213 *Clavus* sp. (Turridae)
214 *Columbella (Atilia) conspersa* Gaskoin (Pyrenidae)
215 *Conuber conica* (Lamarck) (Naticidae)
216 *Daphnella cheverti* Hedley (Turridae)
217 *Diali* sp. 1 (Rissoidae)
218 *Diali* sp. 2 (Rissoidae)
219 *Etrema catapasta* Hedley (Turridae)
220 *E. spurca* Hinds (Turridae)
221 *Herpetopoma atratus* Gmelin (Trochidae)
222 *Inquisitor* cf. *lassulus* Hedley (Turridae)
223 *I. metcalfei* Angas (Turridae)
224 *Latirus recuvirostris* (Schub. Wagn.) (Fasciolariidae)
225 *Mesophora bowenensis* Laseron (Triphoridae)
226 *Nassarius pictus* (Dunker) (Nassariidae)
227 *Natica* cf. *colliei* Recluz (Naticidae)
228 *N. vitellus* L. (Naticidae)
229 *Natica* sp. (Naticidae)
230 *Philine angasi* Crosse and Fisher (Philinidae)
231 *Pseudorhaphitoma* cf. *axicula* (Hedley) (Turridae)
232 *Pupa* sp. (Acteonidae)
233 *Reticunassa paupera* Gould (Nassariidae)
234 *Talopia morti* Iredale (Trochidae)
235 Muricid 1 (Muricidae)
236 *"Bedeva" fischerianus (Tapparone canefri)* (Muricidae)
237 Nudibranch 1 (Nudibranchia)
238 Nudibranch 2 (Nudibranchia)
239 'Sea-hare' 1 (Opisthobranchia)
240 'Sea-hare' 2 (Opisthobranchia)
241 Triphorid (Triphoridae)
242 Trochid (Trochidae)
243 ? *Daphnella* sp. (Turridae)

SCAPHOPODA
244 *'Dentalium'*

PELECYPODA
245 *Aerosterigma oxygonum* Sowerby (Cardiidae)
246 *Antigona lamellaris* Schumacher (Veneridae)
247 *Arca (Arca) navicularis* Bruguiere (Pinnidae)
248 *Atrina (Servatrina) pectinata* L. (Pinnidae)
249 *Azorinus abbreviatus* (Gould) (Solecurtidae)
250 *Chama fibula* Reeve (Chamidae)
251 *C. pulchella* Reeve (Chamidae)
252 *Chlamys (Annachlamys) leopardus* Reeve (Pectinidae)
253 *C. (Chlamys) gloriosa* Reeve (Pectinidae)
254 *C. (C.) grossiana* Iredale (Pectinidae)
255 *Circe sugillata* Reeve (Veneridae)
256 *Clementia strangei* Reeve (Veneridae)
257 *Crytomya cf. elliptica* A. Adams (Myidae)
258 *Cycladicama (Toralimysia)* sp. (Ungulinidae)
259 *Decatopecten (Decatopecten) strangei* Reeve (Pectinidae)
260 *Diplodonta (Zemysina)* sp. (Ungulinidae)
261 *Dosinia (Dosinia) cf. sculpta* Hanley (Veneridae)
262 *'Modiolus' ostenatus* Iredale (Mytilidae)

263 *Ensiculus hilaris* Iredale (Cultellidae)
264 *Eufistulina* sp. (Teredinidae)
265 *Fulvia* sp. (Cardiidae)
266 *Gari (Gari) cf. simplex* Sowerby (Psammobiidae)
267 *Gari venta* Iredale (Psammobiidae)
268 *Gari* sp. (Psammobiidae)
269 *Laternula vagina* (Reeve) (Laternulidae)
270 *Leptomya pura* Angas (Semelidae)
271 *L. cf. pura* Angas (Semelidae)
272 *Limaria (Limaria) cf. delicatuta* Iredale (Limidae)
273 *Lunulicardia subretusum* (Sowerby) (Cardiidae)
274 *Macoma cf. donaciformis* Deshayes (Tellinidae)
275 *Macoma (Salmacoma) cf. vappa* Iredale (Tellinidae)
276 *Macoma* sp. 1 (Tellinidae)
277 *Macoma* sp. 2 (Tellinidae)
278 *Mactra (Electromactra) angulifera* Deshayes (Mactridae)
279 *Malleus albus* Lamarck (Malleidae)
280 *Modiolus micropterus* Deshayes (Mytilidae)
281 *'Modiolus' cf. pulvillus* Iredale (Mytilidae)
282 *Musculus cumingiana* Reeve (Mytilidae)
283 *Neosolen correctus* Iredale (Cultellidae)
284 *Notocorbula hydropica* Iredale (Corbulidae)
285 *Nucula (Leionucula) astricta* Iredale (Nuculidae)
286 *N. (L.) orekta* Iredale (Nuculidae)
287 *Ostrea cf. cristagalli* L. (Ostreidae)
288 *Paphia gallus* Gmelin (Veneridae)
289 *P. subrugata* Iredale (Veneridae)
290 *P. (Paphia) textile* Gmelin (Veneridae)
291 *P. (P.) undulata* Born (Veneridae)
292 *P. (P.) cf. undulata* Born (Veneridae)
293 *Phragmorisma* sp.? (Thraciidae)
294 *Pinctada albina sugillata* Reeve (Pteridae)
295 *Pinna* sp. (Pinnidae)
296 *Placamen sidneyense* (Menke) (Veneridae)
297 *P. tiara* (Dillwyn) (Veneridae)
298 *Regozara flava* L. (Cardiidae)
299 *Scapharea (Cunearca) hubbardi* (Iredale) (Arcidae)
300 *Solecurtis* sp. (Solecurtidae)
301 *Solen vagina* L. (Solenidae)
302 *Spondylus wrightianus* Crosse (Spondylidae)
303 *Syndosmya* sp. (Semelidae)
304 *Tapes (Tapes) watlingi* Iredale (Veneridae)
305 *Tellina (Semelangulus)* cf. *brazieri* Sowerby (Tellinidae)
306 *T. (S.) lilium* Hanley (Tellinidae)
307 *T. (S.) semitorta* Sowerby (Tellinidae)
308 *T. (S.)* cf. *solenella* Deshayes (Tellinidae)
309 *Tellina* sp. (Tellinidae)
310 *T. (Laciolena) texturata* Sowerby (Tellinidae)
311 *Tepidoleda* sp. (Nuculanidae)
312 *Tigamnona chemnitzi* Hanley (Veneridae)
313 *Timoclea (Glycodonta) cf. subnodulosa* Hanley (Veneridae)
314 *Trichomya hirsuta* (Lamarck) (Mytilidae)
315 *Trisidos trisidos* L. (Arcidae)

316 *Tucetilla tenuicostata* (Reeve) (Glycymeridae)
317 Aloidid
318 Venerid 1
319 Venerid 2
320 Bivalve E
321 Bivalve H
322 Bivalve I
323 Bivalve J
324 Bivalve Z

POLYZOA
325 Polyzoan

ECHIUROIDEA
326 *Listriolobus bulbocaudatus* Edmonds

SIPUNCULIDAE
327 *Aspidosiphon* sp.
328 *Golfingia longirostris* (Wesenburg-Lund)
329 *Sipunculus* sp.
330 *Thermiste* sp.

PHORONIDAE
331 Phronid 1
332 Phronid 2

BRANCHIOPODA
333 *Lingula tumidula* Reeve

PHYLUM UNCERTAIN
334 species 1
335 species 2
336 species 3
337 species 4

ECHINODERMATA
ASTROIDEA
338 *Luidia* sp.
339 Sea star
OPHIUROIDEA
340 *Amphioplus depressus* (Ljungman)
341 *Amphipholis loripes* Koehler
342 *Amphioplus* sp.
343 *Amphiura bidentata* H. L. Clark
344 *A. catephes* H. L. Clark
345 *A. magnesquama* H. L. Clark
346 *A. octacantha* H. L. Clark
347 *A. septemspinosa* H. L. Clark
348 *A. tenuis* H. L. Clark
349 *Amphiura* sp.
350 *Ophiacantha confusa* Koehler
351 *Ophiactis perplexa* Koehler
352 *O. savignyi* Müller and Troschel
353 *Ophiactis* sp.
354 *Ophiocentrus* sp.
355 *Ophionephthys* sp.

356 *Ophionereis stigma* H. L. Clark
357 *Ophiothrix stelligera* Lyman
358 *Ophiura kinbergi* Ljungman

ECHINOIDEA

359 *Brissopsis luzonica* (Gray)
360 *Hypselaster jukesii* (Gray)
361 *Salmacis belli* Döderlein

HOLOTHURIOIDEA

263 *Holothuria spinifera* Theel
363 *Mensamaria intercedens* (Lampert)
364 *Protankyra* sp.
365 *Thyone papuensis* Theel

TUNICATA

366 *Adagnesia opaca* Kott (Agnesiidae)
367 *Agnesia glaciata* Michaelson (Agnesiidae)
368 *Aplidium* sp. (Polyclinidae)
369 *Ascidia aclara* Kott (Ascidiidae)
370 *A. sydneyensis* Stimpson (Ascidiidae)
371 *Botrylloides nigrum* Herdman (Styelidae)
372 *Cnemedocarpa floccosa* Sluiter (Styelidae)
373 *Eugyra moretonensis* Kott (Molgulidae)
374 *Microcosmus australis* Herdman (Pyuridae)
375 *M. exasperatus* Heller (Pyuridae)
376 *M. nichollsi* Kott (Pyuridae)
377 *M. spinifera* Herdman (Pyuridae)
378 *M. stolonifera* Kott (Pyuridae)
379 *Microcosmus* sp. (Pyuridae)
380 *Molgula diversa* Kott (Molgulidae)
381 *M. exigua* Kott (Molgulidae)
382 *M. rima* Kott (Molgulidae)
383 *M. mollis* Herdman (Molgulidae)
384 *M. sphaera* Kott (Molgulidae)
385 *Polycarpa fungiformis* Herdman (Styelidae)
386 *P. pedunculata* (Heller) (Styelidae)
387 *P. tinctor* (Quoy and Gaimard) (Styelidae)
388 *Pyura vittata* Stimpson (Styelidae)
389 *Styela plicata* Lesuer (Styelidae)
390 *S. ramificata* Kott (Styelidae)
391 *S. stolonifera* (Herdman) (Styelidae)
392 *Sycozoa pedunculata* Quoy and Gaimard (Clavelinidae)

BALANOGLOSSIDAE

393 *Glossobalanus hedleyi* Hill

CEPHALOCHORDATA

394 *Branchiostoma moretonensis* Kelly

ALGAE

395 *Acetabularia caliculus* Quoy and Gaimard
396 *Asparagopsis taxiformis* (Delile) Collins and Hervey
397 *Ceramium* sp.
398 *Champia parvula* (C. Ag.) Harv.
399 *Chondria* sp.

400 *Dictyota dichotoma* (Huds.) Lamx. var *intricata* (G. Ag.) Grev.
401 *Gracilaria textorii* (Suringar) De Toni
402 *G. verrucosa* (Huds.) Pap.
403 *Gracilaria* sp.
404 *Griffithsia* sp.
405 *Hypnea cervicornis* J. Ag.
406 *Hypnea* sp.
407 *Laurencia rigida* J. Ag.
408 *Laurencia* sp.
409 *Martensia* sp.
410 *Microcoleus lyngbyaceus* (Kuetz.) Crow
411 *Polysiphonia macrocarpa* Harv.
412 *Polysiphonia* sp.
413 *Pseudocodium* sp.
414 *Solieria robusta* (Grev.) Kylin
415 *Solieria* sp.
416 *Sporochnus cosmosus* C. Ag.
417 *S. harveyanus* J. Ag.
418 *Spyridia filamentosa* (Wulf.) Harv.

ANGIOSPERMA

419 *Halophila ovalis* (R. Br.) Hook F.
420 *H. spinulosa* (R. Br.) Aschers

REFERENCES CITED

(These exclude references to authors of species descriptions.)

BIRKETT, L., 1953. Changes in the composition of the fauna of the Dogger Bank area. *Nature, Lond.* **171**: 265.

CHACE, F. A., 1969. Unknown species in the sea. *Science, N.Y.* **163**: 1271.

DAHL, F., 1908. Die Lycosiden oder Wolfspinnen Deutschlands und ihre stellung im Haushalte der Natur. *Nova Acta Leop. Carol. Dtsch Akad. Naturforsch.* **88**: 174–6.

DAY, J. H., FIELD, J. G. and MONTGOMERY, MARY P., 1971. The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *J. anim. Ecol.* **40**: 93–123.

DEAN, D. and HASKIN, H. H., 1964. Benthic repopulation of the Raritan river estuary following pollution abatement. *Limnol. Oceanogr.* **9**: 551–63.

EDDEN, ANNE C., 1971. A measure of species diversity related to the lognormal distribution of individuals among species. *J. exp. mar. Biol. Ecol.* **6**: 199–209.

EMERSON, A., 1939. Social co-ordination and the super-organism. *In* T. JUST (Ed.), 'Animal and Plant Communities.' *Proc. Conf. Amer. Midl. Nat.* **21**: 182–209.

FISCHER, A. G., 1960. Latitudinal variations in organic diversity. *Evolution* **14**: 64–81.

FORD, E., 1923. Animal communities of the level sea-bottom in waters adjacent to Plymouth. *J. mar. biol. Ass. U.K.* **13**: 164–224.

HAILSTONE, T. S., 1972. 'Ecological Studies on the Sub-Tidal Benthic Macrofauna at the Mouth of the Brisbane River.' Ph.D. thesis (Unpublished), Zoology Department, University of Queensland.

HAILSTONE, T. S. and STEPHENSON, W., 1961. The biology of *Callianassa (Trypaea) australienensis* Dana 1852 (Crustacea, Thalassinidae). *Pap. Dep. Zool. Univ. Qd* **1** (12): 259–85.

HENDRICKSON, J. A., JR. and EHRLICH, P. R., 1971. An expanded concept of 'species diversity'. *Notulae Naturae* **439**: 1–6.

HESSE, R., 1924. 'Tiergeographie auf Okologischer Grundlage.' Pp. i–xii, 1–613. (Fisher: Jena).

HOLME, N. A., 1950. The bottom fauna of the Great West Bay. *J. mar. Biol. Ass. U.K.* **29**: 163–83.

1953. The biomass of the bottom fauna in the English Channel off Plymouth. *J. mar. Biol. Ass. U.K.* **32**: 1–49.

1964. Methods of sampling the benthos. Pp. 171–260, *in* 'Advances in Marine Biology', Vol. 2, (Academic Press: New York).

HURLBERT, S. H., 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577–86.

JONES, M. L., 1961. A quantitative evaluation of the benthic fauna off Point Richmond, California. *Univ. Calif. Publ. Zool.* **67**: 219–320.

KITAMORI, R., 1950. Studies on the benthos of Tokyo Bay (II). On the distribution and seasonal change of the benthos (Japanese and English abstract). *Bull. Jap. Soc. scient. Fish.* **16**: 275–80.

KLOPFER, P. H. and MACARTHUR, R. H., 1961. On the causes of tropical species diversity: niche overlap. *Am. Nat.* **95**: 223–6.

KOTT, P., 1972. Some sublittoral ascidia in Moreton Bay and their seasonal occurrence. *Mem. Qd Mus.* **16** (2): 233–60.

KÜHLMORGEN-HILLE, G., 1965. Qualitative und quantitative Veränderungen der Bodenfauna der Kieler Bucht in den Jahren 1953–65. *Kieler Meeresforsch.* **21**: 167–91.

KULLBACK, S., 1968. 'Information Theory and Statistics'. Pp. 1–399, (Dover: New York).

KULLBACK, S., KUPPERMAN, M. and KU, H. H., 1962. Tests for contingency tables and Markov chains. *Technometrics* **4**: 573–608.

LANCE, G. N. and WILLIAMS, W. T., 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. *Comput. J.* **9**: 373–80.

LLOYD, M., 1967. Mean crowding. *J. anim. Ecol.* **36**: 1–30.

LLOYD, M. and GHELARDI, R. J., 1964. A table for calculating the 'equitability' component of species diversity. *J. anim. Ecol.* **33**: 217–25.

LLOYD, M., ZAR, J. H. and KARR, J. R., 1968. On the calculation of information-theoretical measures of diversity. *Am. Midl. Nat.* **79**: 257–72.

LONGHURST, A. R., 1958. An ecological survey of the West African marine benthos. *Fish. Publ. Colon. Off.* pp. 1–102.

MACARTHUR, R. H., 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* **36**: 533–6.

MACARTHUR, R. H. and MACARTHUR, J. W., 1961. On bird species diversity. *Ecology* **42**: 594–8.

MACARTHUR, R. H. and WILSON, E. O., 1967. 'The Theory of Island Biogeography' pp. 1–203 (Univ. Princeton Press: Princeton).

MCINTOSH, R. P., 1967. An index of diversity and the relation of certain concepts to diversity. *Ecology* **48**: 392–404.

MARGALEF, R., 1951. Diversidad de especies en las communicades naturales. *Publicaciones de Instituto de Biologia Aplicada, Universidad de Barcelona* **6**: 59–72.

MAXWELL, W. G. H., 1970. The sedimentary framework of Moreton Bay, Queensland. *Aust. J. mar. freshw. Res.* **21**: 71–88.

MILLS, E. L., 1969. The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. *J. Fish. Res. Bd Can.* **26** (6): 1415–28.

MÖBIUS, K., 1877. 'Die Auster und die Austerwirtschaft', Berlin. (Transl., 1880, The Oyster and Oyster Culture. *Rept U.S. Fish. Comm.* **1880**: 683–751).

MOORE, H. B., 1933. A comparison of the sand fauna of Port Erin Bay in 1900 and 1933. *Proc. malac. Soc. Lond.* **20**: 285–94.

NEWELL, B. S., 1971. The hydrological environment of Moreton Bay, Queensland, 1967–1968. *Div. Fish. Oceanogr. Tech. Pap.* No. 30, 35 pp., (C.S.I.R.O.: Melbourne).

NOY-MEIR, I., 1970. 'Component analysis of semi-arid vegetation in southeastern Australia.' Pp. i–ix, 1–371, Appendix 1–15. Ph.D. Thesis (Unpublished), Australian National University, Canberra.

ORLOCI, L., 1968. Information analysis in phytosociology: partition, classification and prediction. *J. Theoret. Biol.* **20**: 271–84.

PARKER, R. H., 1955. Changes in the invertebrate fauna, apparently attributable to salinity changes in the bays of Central Texas. *J. Paleont.* **29** (2): 193–211.

PEARSON, T. H., 1970. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. I. The physical environment and the distribution of the macrobenthic fauna. *J. exp. mar. Biol. Ecol.* **5**: 1–34.

PETERSEN, C. G. J., 1914. Valuation of the sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. *Rep. Dan. Biol. Sta.* **21**: 1–44, Appendix 24 pp.

PIANKA, E. R., 1966. Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* **100**: 33–46.

PIELOU, E. C., 1966. Species-diversity and pattern-diversity in the study of ecological succession. *J. Theor. Biol.* **10**: 370–83.

1969. 'An Introduction to Mathematical Ecology.' Pp. viii + 286, (Wiley, Interscience: New York).

POULSEN, E. M., 1951. Changes in the frequency of large bottom invertebrates in the Limfjord in 1927–50. *Rep. Dan. biol. Sta.* **53**: 17–35.

RAYMONT, J. E. G., 1949. Further observations on changes in the bottom fauna of a fertilised sea-loch. *J. mar. biol. Ass. U.K.* **28**: 9–19.

RAPHAEL, Y. IRENE and STEPHENSON, W., 1972. The macrobenthic fauna of Bramble Bay, Moreton Bay, Queensland. I. Preliminary studies. *Rept to Comm. Dept Works and Qd Dept Coord. General,* Oct. 1972, 32 pp.

RECHER, H. F., 1972. Bird species diversity: a review of the relation between species number and environment. *In* 'Quantifying Ecology'. *Proc. ecol. Soc. Aust.* **6**: 135–52.

RESVOY, P. D., 1924. Zur definition des Biocönose—Begriffs. *Russk. gidrobiol. Zh.* **3**: 204–209.

SANDERS, H. L., 1968. Marine benthic diversity: a comparative study. *Am. Nat.* **102**: 243–282.

SANDISSON, E. E. and HILL, M. B., 1959. The annual repopulation of Lagos Harbour by sedentary marine animals. *In* SEARS, MARY, 'Reprints of the 1st International Oceanographic Congress, 31st Aug–12th Sept, 1959'. Pp. 584–5, (AAAS: Washington).

SEGESTRÅLE, S. G., 1960 Fluctuations in the abundance of benthic animals in the Baltic area. *Comment. biol.* **23** (9): 1–19.

SIMPSON, E. H., 1949. Measurement of diversity. *Nature, Lond.* **163**: 688.

SLACK-SMITH, R. J., 1960. An investigation of coral deaths at Peel Island, Moreton Bay, in early 1956. *Pap. Dep. Zool. Univ. Qd* **1**: 211–22.

STAUFFER, R., 1937. Changes in the invertebrate community of a lagoon after disappearance of eel grass. *Ecology* **18**: 427–31.

STEPHENSON, W., 1968. The effects of a flood upon salinities in the southern portion of Moreton Bay. *Proc. R. Soc. Qd* **80**: 19–34.

STEPHENSON, W., 1973. The validity of the community concept in marine biology. *Proc. R. Soc. Qd* **84** (7): 73–86.

STEPHENSON, W. and REES, MAY, 1965a. Ecological and life history studies of a large foraminiferan (*Discobotellina biperforata* Collins, 1958), from Moreton Bay, Queensland. I. Life cycle and nature of the test. *Pap. Dep. Zool. Univ. Qd* **2** (10): 207–23.

1965b. Ecological and life history studies of a large foraminiferan (*Discobotellina biperforata* Collins, 1958), from Moreton Bay, Queensland. II. Aquarium observations. *Pap. Dep. Zool. Univ. Qd* **2** (12): 239–58.

STEPHENSON, W. and WILLIAMS, W. T., 1971. A study of the benthos of soft bottoms, Sek Harbour, New Guinea, using numerical analysis. *Aust. J. mar. Freshw. Res.* **22**: 11–34.

STEPHENSON, W., WILLIAMS, W. T. and COOK, S. D., 1972. Computer analyses of Petersen's original data on bottom communities *Ecol. Monogr.* **42** (4): 387–415.

STEPHENSON, W., WILLIAMS, W. T. and LANCE, G. N., 1970. The macrobenthos of Moreton Bay. *Ecol. Monogr.* **40**: 459–94.

STEVEN, G. A., 1930. Bottom fauna and the food of fishes. *J. mar. Biol. Ass. U.K.* **16**: 677–705.

THORSON, G.,1952. Zur jetzigen Lage der marinen Bodentier-Ökologie. *Verh. dtsch. zool. Ges.* **1951**: 115–37.

1957. Bottom communities (sublittoral or shallow shelf). *In* HEDGPETH, J. W., (Ed.), 'Treatise on Marine Ecology and Palaeontology' Vol. I., Ecology. pp. 461–534. *Mem. Geol. Soc. Amer.* **67**. (1963 reprint).

TULKKI, P., 1965. Disappearance of the benthic fauna from the basin of Borholm (S. Baltic) due to oxygen deficiency. *Cah. biol. mar.* **6**: 455–63.

URSIN, E., 1952. Changes in the composition of the bottom fauna of the Dogger Bank area. *Nature, Lond.***170**: 324.

WHITTAKER, R. H., 1965. Dominance and diversity in land plant communities. *Science, N.Y.* **147**: 250–60.

1972. Evolution and measurement of species diversity. *Taxon* **21**: 213–51.

WILLIAMS, W. T., LANCE, G. N., DALE, M. B. and CLIFFORD, H. T., 1971. Controversy concerning the criteria for taxonometric strategies. *Comput. J.* **14** (2): 162–5.

WILLIAMS, W. T., LANCE, G. N., WEBB, L. J. and TRACEY, J. G., 1973. Studies in the numerical analysis of complex rain-forest communities. VI. Models for the classification of quantitative data. *J. Ecol.* **61** (1): 47–70.

WILLIAMS, W. T., and STEPHENSON, W., 1973. The analysis of three-dimensional data (sites × species × times) in marine ecology. *J. exp. mar. Biol. Ecol.* **11**: 207–27.

YAMAMOTO, G., 1952. Seasonal changes of benthonic communities and the succession in the benthos caused by the production of the scallop (Japanese with English abstract). *Sci. Rep. Tohoku Univ. Sci.* (4) **19** (4): 302–14.